KU Leuven
Humanities and Social Sciences Group
Institute of Philosophy

University of Antwerp
Faculty of Science
Department of Biology

ART AND SIGNALING IN A CULTURAL SPECIES

Jan VERPOOTEN

Supervisors:

Prof. A. De Block
Prof. S. Dewitte
Prof. M. Eens

Dissertation presented in partial fulfilment of the requirements for the degree of Doctor in Philosophy and the degree of Doctor in Biology

March 2015

Nederlandstalige titel:

Kunst en signaleren in een culturele soort

Acknowledgments

Eerst en vooral wil ik mijn promotoren bedanken, Andreas De Block, Siegfried Dewitte, Marcel Eens en Mark Nelissen. Andreas, Ik heb veel aan je te danken. Je hebt me geholpen met het vinden van ondersteuning voor mijn onderzoek, eerst bij het Konrad Lorenz Instituut en vervolgens via het FWO-Project dat we samen met Siegfried opstelden. Bedankt voor je gulle feedback, zelfs nog voor je mijn promotor was, op ideeën, papers en projectaanvragen. En ook voor de geweldige hulp bij het finaliseren van deze dissertatie. Siegfried, het grootste deel van mijn doctoraat heb ik doorgebracht in jouw onderzoeksgroep. Ik vond het fantastisch onder jouw vakkundige begeleiding experimenteel onderzoek te kunnen doen - bedankt dat je de tijd genomen hebt om me telkens weer op weg te helpen. Ik hoefde nooit lang te wachten op je uitgebreide feedback die niettemin veel ruimte liet om eigen keuzes te maken. De vele brainstormsessies die we hebben gehouden vond ik steeds inspirerend. Je hebt me vrijheid en kansen gegeven (onder andere om niet-empirische papers af te werken), en mede daardoor bleef het voor mij altijd een plezier om aan dit doctoraat te werken. Marcel, bedankt om me te laten meedraaien in de onderzoeksgroep ethologie en voor de toffe gesprekken over mijn doctoraatsonderzoek en het academische reilen en zeilen. Bedankt om het promotorschap van Mark over te nemen toen hij op pre-emeritaat ging. Ook Rianne bedankt voor de gesprekken, om mee het FWO-project te realiseren en me te introduceren in de onderzoeksgroep ethologie. Mark, aanvankelijk werkten we samen aan een project dat een doctoraat *in* de kunsten zou worden over de biologie van kunst. Uiteindelijk is het geen doctoraat in de kunst maar *over* kunst geworden, niettemin vanuit Darwinistisch oogpunt. Bedankt voor de verschillende interessante gesprekken over de biologische benadering van kunst en voor de raadgevingen omtrent doctoreren.

Verder wil ik Werner Callebaut bedanken voor de warme ontvangst in het Konrad Lorenz Instituut in Altenberg bij Wenen. Het was fijn dat je je persoonlijk bekommerde om de fellows en dat je je steeds ten volle inzette om iedereen verder te helpen. Bedankt voor de steun en de gezellige etentjes. Ik zal dat niet vergeten Werner, R.I.P. I also would like to thank Gerd Müller and Eva Karner of the KLI.

Furthermore, I want to thank all my colleagues that I have encountered in the course of this research for the enjoyable times we had. I'd like to thank the colleagues at the Konrad Lorenz Institute: office mates Wayne and Brett, Alejandro, Istvan, Miles, Eran, Ellen, Rachael, Naomi, Elisa, Aida, Daniel, Laura, Matthias and Christine. Thanks for the drinks, diners, talks, and walks, etc. I'd also like to thank the colleagues at the Research center for Marketing and Consumer Science in Leuven for fun times, office discussions and so on: office mates Sam, Huiying, Olga, and Maja; and Aiste, Andrea, Angelos, Anouk, Dion, Efty, Hannelore, Inge, Jamie, Jan, Justin, Karolien, Laure, Lien, Luk, Michelle, Sabrina, Yannick and Zeynep. Also thanks to office mates at the ethology lab at the University of Antwerp: Anke, David and Stefania; and Morgan. Finally, also thanks to the colleagues from The Centre for Logic and Analytic Philosophy in Leuven.

Yannick, onze papers zijn een aanzienlijk deel van deze dissertatie geworden. Bedankt om de paper over religieuze monumentale architectuur te trekken. Veel tijd en moeite hebben we erin gestoken, maar het heeft uiteindeijk geloond en het is een stuk van monumentale omvang geworden. Ik apprecieer het ook zeer dat je steeds hebt klaargestaan met een luisterend oor, bemoedigingen en advies. Stefaan, merci voor het mee organiseren van onze workshop. Hopelijk wordt de follow-up even fijn. Dear Derek, thanks for the fine collaboration on our paper. Isabelle, bedankt voor alles dat je gerereld hebt, altijd flexibel en gezwind. I am also grateful to everyone who gave feedback on the papers that comprise this thesis. They are mentioned at the end of each of the chapters.

Vrienden en familie, de wetenschap dat ik op jullie kan rekenen is goud waard. Bedankt om interesse te hebben getoond in de voortgang van mijn onderzoek – papa je hebt alles steeds op de voet gevolgd. Mama en papa, de manier waarop jullie in het leven staan, onderzoekend en met kritisch engagement, is een bron van inspiratie voor mij. Ook wil ik ouders én schoonouders, bedanken om er voor ons te zijn, en voor alle hulp met huis en kind. Zonder jullie hadden we het niet gerooid.

Asa, mijn zoon, ik had verwacht dat je komst zou interfereren met mijn werk. Niets was minder waar. Je stralende aanwezigheid geeft me elke dag meer moed en energie dan ik ooit had - ook al neem je me vaak mijn nachtrust af! Els, je was er vanaf het begin bij. Je hebt me de kans gegeven twee jaar naar Wenen te gaan. Vervolgens zijn we samen de uitdagingen aangegaan die de nieuwe levensfase van kind en huis meebrengt. Met jou heb ik alles gedeeld, de frustraties, de twijfels, maar ook de roes als iets goed was gegaan. Je leefde en dacht met me mee en stond me bij met bedachtzame raad zoals alleen jij dat kan. Ik hoop dat ik hetzelfde kan doen voor jou tijdens het verdere verloop van jouw doctoraat en alle andere dingen die je nog wil doen. Ik zie je graag.

Contents

Figures

Tables

General Introduction

Putting a cultural product we hold dearly, such as wine, to the test can be sobering. In the last few decades, wine preferences and connoisseurship have been empirically verified which has led to some thought-provoking findings. Several studies suggest that expert wine judgments are unreliable and inconsistent. Morrot et al. (2001) showed that wine experts are unable to distinguish between a red and a white wine. When a white wine was dyed with food coloring, wine experts described it in language typically reserved for characterizing reds. They called it "jammy," for example, and noted the flavors imparted by its "crushed red fruit." In addition, while most wine critics routinely report tasting six or more flavors (red plums, cobbler, cinnamon, star anise, blackberry bramble, whole black peppercorn, etc.), they cannot reliably identify more than three or four of a wine's flavor components (Mlodinow, 2009). Furthermore, Hodgson recently demonstrated inconsistencies in expert judgments. In one study, Hodgson (2008) had judges at California State Fair wine competition – the oldest and most prestigious in North America -, blindly taste the same wine three times in succession. The judges' ratings typically varied by ±4 points on a standard ratings scale running from 80 to 100. Another study, involving more than 4000 wines and 13 U.S. wine competitions, revealed that whether a wine wins a Gold medal is greatly influenced by chance as winning a Gold medal at one competition turned out to be stochastically independent of the probability of receiving a Gold medal at another competition (Hodgson, 2009). Even more surprising may be the finding that wine expert taste preferences are opposite to those of amateur wine drinkers. In a large survey with blind tastings, Goldstein et al. (2008) found a negative correlation between price and enjoyment for amateurs, while they found a positive trend between price and enjoyment among experts. In summary, these findings suggest that wine expert perceptual judgments are rather arbitrary except in their consistent deviation from the tastes of the general audience.

The picture that these scientific findings on wine tasting expertise paint, illustrates a few issues of relevance to this dissertation about the evolution of the arts. First, we may wonder about whether the found patterns apply to the appreciation of other cultural products, such as art, as well. Are prestigious art experts reliable? From the viewpoint of the outsider, what experts assert is normally beyond our reach to verify. We are left to take their word for it. The same may apply with regard to art. The recently deceased art expert, multiple museum director and curator Jan Hoet (perhaps most known for curating Documenta IX in Kassel in 1992) famously sensed the Zeitgeist before it was well established and discovered several artists who later acquired world fame (e.g., painter Luc Tuymans). However, Hoet's authority has sometimes been questioned, both by art professionals and the general audience. Some people suggested that he was *creating* Zeitgeist rather than sensing it. Most importantly, it was sometimes unclear why he extolled one artist and not another one. In Flanders he used to be called "pope of art", a title that nicely illustrates the rather mystic criteria he used to judge art.

Were Hoet's judgments about art difficult to grasp because he had the ability to perceive aspects about art most people don't, or was it because his judgments were rather arbitrary, just as wine experts' judgments appear to be? Empirical research on art appreciation and expertise may help elucidating the reliability and consistency of art expert judgments (see General Discussion: Future Directions). Chapter 8 of this thesis reports studies we conducted that do not directly settle this issue but that do show some interesting parallels between art and wine expertise and appreciation. For example, we tested whether people take into account prestige when judging artworks. Participants were either told that the artworks they were going to judge belonged to the MoMA (Museum of Modern Art in NY, one of the most prestigious art museums in the world) or they were not given any context information about the artworks. We found that experts who were told that the artworks belonged to the MoMA conferred higher appreciations to the artworks than experts that were not given any context information about the same artworks. This suggests that experts judge artworks, independent of inherent quality, more favorably merely on the basis of prestige. Laypeople, in contrast, were not affected by the prestige manipulation. We also verified whether experts' and laypersons' appreciations were differently affected by the attractiveness of the content of artworks (neutrally attractive faces vs. very attractive faces). Our results indicated that laypeople and experts have opposite preferences when it comes to art (laypeople preferred art depicting very attractive faces while experts preferred neutrally attractive), which is strikingly similar to the results revealed on wine appreciation by Goldstein et al. (2008). The similarity of these patterns raises the question whether they reflect a more fundamental process in preference evolution shared by the wine domain and the art domain (see General Discussion: Future Directions).

The wine studies also reveal a more general issue: how does one guarantee the reliability and validity of expert judgments? One obvious answer is to let experts gain more experience. However, that does not appear sufficiently. The scientific study of expertise in general and in specific domains, can help with that. For example, it is to the benefit of both wine makers and consumers that ranking in competition is based on fair evaluations, as prices depend on it. Unveiling the arbitrariness of wine ranking in such prestigious competitions, as was realized by Hodgson's analyses (2008), should diminish the unfair impact on prices they have. But science can do this only if she is optimally informed by the expertise itself: not just science about experts but also at least partly (informed) by experts. It is no coincidence that several of the authors of these wine studies are also professional winemakers (Frédéric Brochet, Robert Hodgson, etc.). For the same reason, the study of the evolution of art requires not only the rigor of science, but also an in-depth understanding of art making and appreciation informed by history and philosophy of art and philosophical aesthetics (cf. Bullot & Reber, 2013). I will discuss this further on, when I present the disciplines involved in the evolutionary study of the arts. The next section provides a general theoretical background of this dissertation and highlights a number of divides that play a role in the study of the evolution of the arts. Finally, I introduce the three main parts (together comprising eight chapters) of this dissertation.

Theoretical background

There are a number of divides research on the evolution of the arts is confronted with which I will briefly discuss here: academic and intellectual divides between disciplines, the divides between art making and appreciating, between art with a capital a and popular art, and between different arts.

Three cultures

In the fifties of the previous century Snow (1959) famously lamented a divide between "two cultures" in academic and intellectual life. These were the culture of the (natural) sciences and the culture of the humanities. He denounced the fact that scholars from the respective fields had little to no interest in each other's domains and lacked even the most basic knowledge about each other's fields of study. Revisiting Snow, Kagan (2009) recently added a third culture to the picture, the social sciences, and observed that the mutual incomprehension and enmity between the - now three - cultures had only grown since Snow's time.

Against this cultural backdrop, the study of the evolution of the arts is a very challenging endeavor, since it tends to ignore the academic boundaries guarded by sometimes rather narrow-minded scholars. In his book on the evolution of stories (see Chapter 1), Boyd (2009, p 1-2), an English literature professor, recalls a colleague asking him:

> "What are you working on?" "I'm trying to figure out," I answered, "an evolutionary – Darwinian - approach to fiction." Not waiting to hear more, he shut down his face and the conversation: "That must be very reductive." "No, not reductive, but expansive," I might otherwise have answered [.]

I think Boyd is right: the evolutionary study of art is – or at least should be – expansive. In my view, the study of the evolution of the arts is inherently interdisciplinary and spans (or even integrates) the three cultures. This is illustrated by the variety of disciplines that have contributed to the topic: ethology (e.g., Ellen Dissanayake, Desmond Morris, Nancy Aiken, Kathryn Coe), cognitive biology (e.g., Tecumseh Fitch), behavioral ecology (e.g., Richard Prum), neurology (e.g., Marcos Nadal, Vilayanur Ramachandran, Camilo José Cela-Conde), evolutionary psychology (e.g., Leda Cosmides and John Tooby, Geoffrey Miller), linguistics (e.g., Steven Pinker), anthropology (e.g., Michelle Scalise Sugiyama), archeology (e.g., Derek Hodgson), art history (e.g., Olivier Morin, Helen De Cruz), philosophy of art (e.g., Stephen Davies, Dennis Dutton), literature (e.g., Brian Boyd, Joseph Carroll), etc.

The (broadly conceived) evolutionary approach theoretically unites or integrates all these accounts. However, this does not need to imply a colonization - as is sometimes feared -, nor a unidirectional flow of knowledge from natural evolutionary science to the social sciences and humanities. Insights and concepts from the humanities and social sciences are also often used to elucidate and even correct the evolutionary study of human and non-human animal behavior and cognition. Ignoring insights from the humanities about art may lead to distorted (unrealistic) evolutionary hypotheses about art and will meet opposition. This may happen, for example, because they are based on a very naïve image of what (high) art is and how it is appreciated (Bullot & Reber 2013; also see commentaries to Ramachandran & Hirstein 1999). Fortunately, evolutionary students of the arts acknowledge that insights and knowledge from the three cultures are mutually informative.

Thus, it can be said that the study of the evolution of the arts builds bridges between the three cultures. In doing so, it incidentally acquires broader academic relevance in that it sets an example of going against the currently prevailing trend of respect and communication breakdown among the three cultures. It demands an open mind from the three cultures without them having to lose their crucial independence and integrity. In other words, it provides a useful test case for a multi-"cultural" academic and intellectual community.

Of course, the multidisciplinary approach of students of the evolution of the arts is not with out risks. One thing that divides the three cultures and causes incomprehension, as Kagan (2009) notes, is vocabulary, or more specifically, the different meanings the same term may have in different disciplines. For example, "function" is quite rigorously defined in evolutionary biology, which is not always appreciated by humanists who sometimes seem to employ it rather carelessly, for instance, when they seek explanations for the evolution of fictional storytelling (see Chapter 2). Moreover, function denotes something very different in evolutionary biology than it does, for instance, in anthropology, which has caused confusion and misunderstanding until today (see Chapter 3).

Another thing that divides the cultures, according to Kagan (2009), are the differences in primary concerns. The problem of differing concerns can be observed in relation to the use of the term adaptation. An adaptive trait of an organism is a trait that has been shaped by natural selection and/or sexual selection on account of the beneficial effect(s) it has in terms of survival and/or reproductive success. An adaptation as such is actually something that is only of interest for the biological evolution of art. The humanities are not really interested in adaptation directly; their primary concerns are more about the human condition and the place of art in the good life. From this interest they may presume too easily that adaptation and value are closely linked. Obviously, this is wrong. For example, there are some indications that a disposition to develop rape behavior may have been selected for in our ancestral past (at any rate, it appears in animals of distinct taxa, e.g., arachnids, ducks, bottle-nose dolphins and orangutans), but that does not whitewash it at all. Nonetheless, (implicit) value judgments sometimes seem to slip into discussions about whether aspects of human behavior qualify as adaptations or not. For example, most literary Darwinists (humanists employing a Darwinian approach to literary behaviors such as literature and its oral antecedents) consider art an adaptation. Since glorifying art as a key human achievement is inherent part of the tradition of the humanities - and a guaranty for their relevance, this might reflect a bias. Similarly, humanists tend to consider art making and appreciation a uniquely human behavior (e.g., Thierry Lenain, Johan De Smedt, Stephen Davies, Brian Boyd, Eveline Seghers etc.), while biologists tend to favor the opposite premise (e.g., Tecumseh Fitch, Desmond Morris, Richard Prum, also see chapters 4 & 7). Irrespective of who is right, this opposition can to some extent be traced back to the differing backgrounds and concerns. Human uniqueness (as determined by comparison with nonhuman animals and as achieved in art) is an almost perennial humanist premise, while biologists, following Darwin, tend to see species, including humans, as subject to the same fundamental processes as other animals. On the upside, disagreement is crucial to progression. The fact that accounts from all these different backgrounds are in communication with one another may gradually weed out mutual misconceptions and refine comparisons between human and other species, also regarding products of aesthetic evolution across the animal kingdom. In the next subsection, I zoom in on the three disciplines (each belonging to another of the three cultures) I attempt to employ in this thesis to study the evolution of the arts.

Disciplines

In accordance with the general spirit of the emerging evolution of the arts research community, this dissertation combines insights and methods from different disciplines in an attempt to elucidate pending issues regarding evolution and the arts in these disciplines. The main disciplines employed in this thesis are philosophy, biology and psychology (which is also reflected by the backgrounds of the co-authors of some of the chapters).

Philosophy of biology constitutes an important part of the dissertation in two ways (Griffiths, 2014). First, I subject the conceptual puzzle regarding adaptation and alternative explanations of art (as an example of a complex cognitive and behavioral trait) to philosophical analysis (Chapters 1 – 3). Second, I make appeals to biology in discussions of traditional philosophical questions. In Chapters 1, 3, 7 – 8 of the dissertation I address the nature of art and its appreciation as well as its relation to the appreciation of natural beauty, which have been and still are central topics in philosophy of art and philosophical aesthetics. I will employ biology for philosophical purposes in these chapters.

Furthermore, evolutionary biology comprises a major part of this dissertation. Where useful, I make the classic ethological distinction between proximate (mechanism) and ultimate causes (function) of a (behavioral) trait (Chapters 1, 4, and Conclusions). Also, I employ the cross-species comparative method to assess function and evolution (Chapter 4 mainly). I deploy adaptationism, which is considered central to evolutionary biology, and discuss its use at length as mentioned in the previous paragraph. In two chapters, I use niche construction, the process in which on organism modifies its own (or other species') selective environment, to elucidate the evolution of human building behavior and architecture (Chapter 4 - 5). Above all, the dissertation builds heavily on signaling theory, a body of theoretical work examining animal communication. Especially models that originated in sexual selection research, such as Fisher's process, costly signaling, and sensory exploitation are extensively discussed throughout the thesis for their potential use in explaining patterns of cultural transmission (hence the title of this thesis). This is not entirely new. As a matter of fact, Fisher's process and costly signaling have already been borrowed by cultural evolution theory since its inception in the eighties of the previous century (Boyd & Richerson, 1985). However, sensory exploitation was not borrowed by cultural evolutionists - presumably because the model was only developed in the beginning of the nineties. To fill this important gap, several of the chapters of this dissertation primarily explore the explanatory value and power of the sensory exploitation model applied to cultural evolution, more specifically to cultural evolution of visual art and architecture (Chapters 3 – 4, 6 – 8, Conclusions and Appendix 2).

Finally, also psychology accounts for an important part of this dissertation. Evolutionary psychology forms the main framework of several influential accounts on the evolution of art, such as Miller's (2000) sexual display and Pinker's (1997) byproduct hypothesis about art, which are discussed in several chapters (Chapters 3, 7-8, and Appendix 2). Furthermore, Chapter 8 reports empirical research in which experimental psychology methods were employed. Chapter 8, being the final chapter of this dissertation, attempts to combines all three main disciplines. It experimentally tests (psychology) predictions based on signaling theory (evolutionary biology), in an attempt to shed light on pending issues regarding art appreciation and art institutions (philosophy). In the next subsection I address art making and appreciating from a signaling-theory perspective.

Art making and appreciating

Another divide that deserves attention, is the one between art production and appreciation or artist and audience. From a functionalist standpoint, whether the divide occurs or not, depends on the particularities of the hypothesis about art. Some hypotheses regard "art behavior" as a group activity, evolved to strengthen social bonds. In such activities everyone is both artist and audience and the divide disappears. This might apply to artistic activities in the context of rituals typical of ancient and modern hunter gatherers (Dissanayake, 1999; also see chapter 3). Some cognition-focused hypotheses about art may suggest that the only audience required for adaptive benefit is the artist herself, which makes the presence of an external audience functionally redundant (Tooby & Cosmides, 2001). However, other accounts point out that evolutionary benefits associated with art may not always be aligned for artists and audiences. If that is the case, the divide between artist and audience becomes the pivotal issue of the hypothesis.

Signaling theory makes clear what is at stake. If art is information (broadly conceived), sent from artist to audience, it can be understood as a signal from sender to receiver. Signaling theory states that signals evolve because they modify the behavior of the receiver to benefit the signaler (Bradbury & Vehrencamp, 1998). If the interests of senders and receivers are perfectly aligned, as in Dissanayake's (1999) proposal about art, the sender benefits as well. However, when there is a conflict of interest between senders and receivers, an "arms race" between them ensues, where senders attempt to manipulate receivers and receivers attempt to avoid manipulation (Dawkins & Krebs, 1978). Theoretical and empirical research suggests that both manipulation and avoidance of manipulation may occur in transient bouts but they may be stable evolutionary outcomes as well (Johnstone, 2002). Receivers may avoid manipulation and selectively prefer signals that reliably indicate some quality from the sender. This is referred to as honest signaling and implies that not only senders benefit but receivers benefit as well, despite their conflict of interest. Miller's (2000) sexual display hypothesis about art falls within this latter category. The sexual conflict of interest Miller appeals to, arises from the well-documented fact that, in humans as in most other animals, males have larger reproductive variance than females (Bateman's principle). This is a consequence of the fact that (especially mammalian) females almost always invest more energy into producing offspring than males invest. As a result, women have been selected to be choosy. Men may use beautiful art, pushing the female's pleasure buttons to entice her regardless her reserve (i.e., sensory exploitation). However, on Miller's view, women have evolved the counterstrategy to selectively prefer artworks from artists that indicate that they have good genes (i.e., they are artistic geniuses). This kind of choosiness allows them to benefit as well, by helping them to produce high quality offspring with the artist (i.e., "smart choosy daughters" and "sexy artistic sons").

However, cultural evolutionary accounts have put forward that manipulation may occur stably as well and that this manipulation is not limited to mating strategies and thus is sex-independent (which nicely fits the fact that across cultures both men and women are commonly artist and audience) (Sperber & Hirschfeld, 2004; Chapter 3, 7-8; Appendix 2). If artworks (or other cultural artefacts) elicit responses among receivers which are maintained by strong selection for other purposes, receivers may become exploited by these artefacts or their producers. For example, the relative abundance of face stimuli among artefacts (i.e., portraits, masks, caricatures etc.), has been linked to the sensitivity of the face recognition system. Face recognition capacity is under strong positive selection, given its importance in social interaction. The incapacity to detect and read faces is expected to be detrimental for fitness. Therefore, the system is susceptible to false positives i.e., "fake faces," and may result in "a massive cultural exploitation" (Sperber & Hirschfeld, 2004, p. 43). Humans are expected to have several such strong perceptual and cognitive biases maintained by selection and susceptible to exploitation through art, a hypothesis which is explored in detail throughout this dissertation (Chapter 3, 7-8; Appendix 2). In the final chapter, we develop and explore the hypothesis that the "art world" constitutes an audience that may have socially learned to resist exploitation of their biases (also see General Discussion: Future Directions). This might have led to the evolution of art with a capital a, which is discussed in the next subsection.

Art with a capital a versus popular art

When comparing art to wine, I mentioned that experts may have quite different preferences compared to laypeople and that this is not always taken into consideration. One of the most pressing issues regarding art's social and economic status is the difference between popular art and "high" art and their respective appreciation by the general audience and by a smaller number of people with art expertise. Even though judgments about art may vary between individuals, also among experts (Hekkert & van Wieringen, 1998; Leder et al., 2012) high art can be broadly conceived as art that was created for and accepted by an expert audience, the "art world" (Danto, 1995).

Take for example, reactions to Duchamp's ready-made urinal "The Fountain" where an art critique praised "A lovely form has been revealed, (…) there a man has clearly made an aesthetic contribution." while Duchamp aimed to discourage aesthetics writing: "I threw […] the urinal in their faces as a challenge and now they admire them for their aesthetic beauty." (both Danto, 1995, p. 85). This aesthetic ambiguity of this signature piece of modern art, leads to the central—since decades hotly debated—question: Does high-art appreciation reflect some hard-to-assess quality, which can only be appreciated through intensive training and knowledge - or does it rather reflect mere snobbery as a means to acquire status or a badge of elite group membership (Wolfe, 1975; Bullot & Reber, 2013)? Possible answers to this question are discussed theoretically and experimentally assessed in the final chapter of this dissertation (also see General Discussion: Future Directions). When talking about art, people mostly think about visual art with a capital a, but visual art is just one of "the arts," which is a much broader concept that also includes literature (including poetry, novels and short stories, and epic), performing arts (among them music, dance, and theatre) and even culinary arts such as baking, chocolatiering, and winemaking. In the next subsection I will briefly discuss why this broader, more inclusive approach to art, may be useful when employing an evolutionary approach.

Different arts

There are good reasons to consider several of the arts from an evolutionary perspective rather than just focusing on one. First of all, it allows considering the issue whether the arts should or can be evolutionary understood all together, as “art,” or whether they need to be considered each on its own (Chapter 1). Some evolutionary explanations start from some underlying thing or process that all arts may have in common, such as play behavior (Boyd 2009; Chapter 1), artification/making special (Dissanayake , 1999) or sexual display (Miller 2000; Chapter 7, Appendix 2). But it is conceivable that the arts have come to us through various evolutionary pathways, maintained by different uses and (in)direct selection pressures. A further reason to consider several arts is that insights from more intensively studied topics may be used to progress the understanding of less intensively studied ones. Finally, irrespective of the possibility of a unified evolutionary theory about art comprising all arts, any art still has its peculiarities which aren’t shared with other arts and which are nonetheless evolutionary relevant. For example, architecture, next to its aesthetic roles, provides protection against biotic and abiotic hostile forces (which it has in common with animal architecture but not with other arts) (Chapters 4 – 6). Next I introduce the three parts (comprising eight chapters in total) of this thesis.

Introduction to Part I (Chapters 1-3)

In the first chapter of this dissertation I evaluate a currently influential account of the evolution of art, Brian Boyd’s recent book *On the Origin of Stories: Evolution, Cognition, and Fiction* (2009). The book’s main thesis is that art is an adaptation, biologically part of the human species, which derived – in the phylogenetic sense - from adaptive animal play behavior. It offers a stimulating collection of findings, ideas, and hypotheses borrowed from a wide range of research disciplines (philosophy of art and art criticism, anthropology, evolutionary and developmental psychology, neurobiology, ethology, etc.), brought together under the umbrella of evolution. However, Boyd glosses over some issues that should have been cleared before coming to conclusions about the evolution of art. For example, Boyd explicitly lumps together organic and cultural evolution without providing a consistent argumentation why this simplification would be justified. He does not consider alternative explanations to art as adaptation such as exaptation and constraint. Moreover, the neurobiological literature suggests current evidence of biological or cognitive adaptation for most of the arts is weak at best. Given these considerations, I conclude the chapter by proposing to regard the arts instead as culturally evolved practices building on pre-existing biological traits.

In the second chapter I extend some of my concerns with Boyd's account to the emerging field of Literary Darwinism. Literary Darwinism is an interdisciplinary research field that seeks to explain literature and its oral antecedents ("literary behaviors"), from a Darwinian perspective. Considered the fact that an evolutionary approach to human behavior has proven insightful, this is a promising endeavor. However, Literary Darwinism as it is commonly practiced, arguably suffers from some shortcomings. First, while literary Darwinists only weigh adaptation against by-product as competing explanations of literary behaviors, other alternatives, such as constraint and exaptation, should be considered as well. I attempt to demonstrate their relevance by evaluating the evidentiary criteria commonly employed by Literary Darwinists. Secondly, Literary Darwinists usually acknowledge the role of culture in human behavior and make references to Dual Inheritance theory (i.e., the body of empirical and theoretical work demonstrating that human behavior is the outcome of both genetic and cultural inheritance). However, they often do not fully appreciate the explanatory implications of "dual inheritance." Literary Darwinism should be extended to include these recent refinements in our understanding of the evolution of human behavior.

In the third chapter Derek Hodgson and I develop an evolutionary thesis that does take into account the cultural nature of the arts. Furthermore we pay attention to the fact that the arts in ancestral and current hunter-gatherers are mostly inextricable entangled with ritualistic activities. Whether the arts are adaptive or not, thus also depends on whether the rituals the arts serve are. The role of the arts has become crucial to understanding the origins of ''modern human behavior," but continues to be highly controversial as it is not always clear why the arts evolved and persisted. We argue that the arts have evolved culturally rather than biologically, exploiting biological adaptations rather than extending them. In order to support this line of inquiry, we present in this chapter evidence from a number of disciplines showing how the relationship between the arts, evolution, and adaptation can be better understood by regarding cultural transmission as an important second inheritance system. This allows an alternative proposal to be formulated as to the proper place of the arts in human evolution. However, in order for the role of the arts to be fully addressed, the relationship of culture to genes and adaptation need to be explored. Based on an assessment of the cognitive, biological, and cultural aspects of the arts, and their close relationship with ritual and associated activities, we conclude with the null hypothesis that the arts evolved as a necessary but nonfunctional concomitant of other traits. This null hypothesis, we assert, cannot currently be refuted.

Introduction to Part II (Chapters 4-6)

In the following three chapters, Yannick Joye and I attempt to explain varied aspects about architecture from an evolutionary perspective. In chapter 4 we note that, rather than being a recently invented practice, building homes and other architectural constructions, such as temples and monuments, are a perennial part of the human behavioral repertoire, which may have had an important impact on human cultural, genetic, and ecological evolution. Studying architecture from a biological and evolutionary perspective may thus be relevant to the understanding of human evolution; and vice versa, a biological and evolutionary perspective may enhance our understanding of architecture as a crucial part of human life. Yet, human architecture has hardly been investigated from a biological and evolutionary perspective. In this fourth chapter, we aim to contribute to this much-needed approach to architecture. We distinguish and investigate two main purposes of architecture: a protective function (against biotic and abiotic hostile forces), and an intraspecies signaling function. Based on a phylogenetic approach, we speculate that the protective function of architecture has been the main selection pressure on the evolution of human building aptitudes, which in turn may have promoted the evolution of human intelligence and ecological dominance. Contrary to other primate genera, these building aptitudes were, at a later stage in the evolution of Homo, co-opted for artificial signaling. Nonetheless, artificial signaling can also be found in other species, especially in fish and birds, which raises the intriguing question what causes this commonality. We comparatively evaluate three models of signal evolution with respect to architectural aesthetics: arbitrary coevolution, sensory exploitation and costly signaling.

In chapter 5, we extend existing accounts on the evolution of monumental architecture, which primarily focus on genetic evolution, with insights from cultural evolution theory and niche construction. Cultural evolution theory asserts that the behavioral repertoire of humans – unlike that of most nonhuman animals – relies heavily on social learning (Henrich & McElreath, 2003). By enabling the accumulation and retention of locally adaptive cultural innovations, social learning has caused (cultural) adaptation to a wide range of local environments. In addition, humans have also actively modified these environments, which in turn has fed back on cultural and genetic evolution (Odling-Smee, 2010). Architecture constitutes an important part of that modified selective environment (Hansell, 2005; Odling-Smee & Turner, 2012). Given the feedback between genes, culture and constructed environments and considering the fact that social learning is adaptive in humans, in this chapter we explore how human architecture might have evolved to support – or even to galvanize – social learning. More specifically we zoom in on one general kind of architecture, i.e., religious monumental architecture, and try to shed light on how the specific awe-like emotions that can be elicited by such architecture might have impacted cultural evolution. We distinguish between two pathways through which awe-evoking religious monumental architecture may have enhanced cultural transmission between individuals. First, it may have stimulated cognitive performance underlying learning, leading to – for example – enhanced memory, and in so doing, it supported the reception and retention of cultural variants. Second, it may have provided a social background against which social learning could occur. Specifically, we propose that awe-evoking RMA may have caused individuals to become more prosocially oriented towards others (which increased opportunities for social learning) as well as to have contributed to establishing a learning relationship between religious leaders and commoners.

In the sixth chapter, we connect the evolutionary account we developed about architecture to the cognitive science of religion. In recent years, the cognitive science of religion has displayed a keen interest in religions' social function, bolstering research on religious prosociality and cooperativeness. The main objective of this chapter is to explore the biological and psychological mechanisms through which religious monumental architecture might support that specific function. A frequently held view is that monumental architecture is a costly signal that served vertical social stratification in complex large-scale societies. In this chapter we extend that view. We hypothesize that the function(s) of religious monumental architecture cannot be fully appreciated from a costly signaling perspective alone, and invoke a complementary mechanism, namely sensory exploitation. We propose that, in addition to being a costly signal, religious monumental architecture also often taps into an adaptive "sensitivity for bigness." The central hypothesis of this paper is that when cases of religious monumental architecture strongly stimulate that sensitivity, and when commoners become aware of the costly investments that are necessary to build religious monumental architecture, then this may give rise to a particular emotional response, namely awe. We will try to demonstrate that, by exploiting awe, religious monumental architecture promotes and regulates prosocial behavior among religious followers and creates in them an openness to adopt supernatural beliefs.

Introduction to Part III (Chapters 7-8)

The final two chapters of this dissertation zoom in on the evolution of visual art. In chapter 7, Mark Nelissen and I address a conundrum that has puzzled archeologists and art historians (Spivey, 2005): the lag between the rise of anatomically modern humans about 200,000–160,000 years ago and complex art (i.e., figurative imagery and realistic art), which only appeared consistently in the archaeological record about 45,000 years ago. The dominant explanation of this lag has been that due to some assumed genetic mutations a neurocognitive change took place, which led to a creative explosion (in Europe). Recently, insights from cultural evolution theory have allowed formulating an alternative explanation that better fits existing data. One of these data is that realistic art appeared (and disappeared) not only in Europe but in several parts of the world since the Upper Paleolithic / Late Stone Age. Essentially, it seems that the accumulation and retention of innovations required for producing complex artefacts, such as realistic depictions (e.g., learned aspects of drawing skills, pigment processing, charting suitable surfaces, etc.) necessitate a large enough population of socially interacting individuals. Evidence indicates such a demographic change took place in Upper Paleolithic Europe prior to the appearance of figurative cave art, thus providing an alternative explanation for the creative explosion. Existing models assume that socially learned complex behaviors including art making were retained for adaptive purposes (Powell et al., 2009). However, in this chapter, we provide an alternative, more parsimonious (in the relative sense: Sober, 2006), explanation. We propose that art evolved because it exploited preexisting preferences, that were maintained by selection in another context (e.g., face recognition system in the brain exploited by portraits). On this view, figurative art traditions have evolved by piggybacking on cumulative adaptive evolution. We conclude that sensory exploitation is a "primary force" that suffices to drive the evolution of art, but that, depending on identifiable conditions (see discussion Appendix 2), secondary forces may kick in.

In the final chapter of this dissertation, Siegfried Dewitte and I address such a secondary force: *resistance against exploitation*. An important aspect of the exploitative power of art may be that it elicits pleasure by appealing to evolved aesthetic preferences that evolved for other purposes. In line with this, it has been suggested that art is a pleasure technology that evolves by pushing human "pleasure buttons" (Pinker, 1997). Consequently, spectators may trade-off rewards from indulging in art and biological activities, resulting in less effort being allocated to reproduction. We contend that, while the general audience (i.e., laypersons) may indeed be exploited (i.e., content bias), experts (i.e., artists, art critics, museum directors, etc.), who are typically being exposed to high doses of art, may have socially learned to resist exploitation by selectively preferring art from prestigious artists (i.e., prestige bias). The latter would be in line with the claim that prestige bias may trump content biases. The results of three experimental studies support our contention. We found that laypeople's art appreciation is positively affected by a content bias for attractive faces, mediated by aesthetic pleasure, whereas experts' appreciation is positively affected by prestige and mediated by admiration for the artist. Moreover, experts confer lower appreciation to attractive compared to moderately attractive content, which is consistent with our contention that expertise and the use of prestige are associated with resistance against beautiful content that exploits evolved preferences. This research thus suggests that expertise moderates content and context (prestige) biases, which may be of relevance to an ongoing debate about their relative importance as drivers of cultural evolution. In addition, this study provides a tentative but novel explanation for the fact, famously established by philosopher Arthur Danto (2003), that beauty lost its central position in Western art during the 20th century.

References

Boyd, B. (2009). *On the origin of stories: evolution, cognition and fiction.* Belknap Press of Harvard University Press, Cambridge

Boyd, R., & Richerson, P. J. (1985). Culture and the evolutionary process. *University of Chicago, Chicago*.

Bradbury, J. W., & Vehrencamp, S. L. (1998). Principles of animal communication. *Sinauer, Sunderland*

Bullot, N. J., & Reber, R. (2013). The artful mind meets art history: Toward a psycho-historical framework for the science of art appreciation. *Behavioral and Brain Sciences*, *36*(02), 123–137. doi:10.1017/S0140525X12000489

Danto, A. C. (1995). *After the end of art. Contemporary art and the pale of history*. Princeton, New Jersey: Princeton University Press.

Danto, A. (2003). *The abuse of beauty: aesthetics and the concept of art*. Chicago: Open Court.

Dawkins, R., & Krebs, J. R. (1978). Animal signals: information or manipulation? In: *Behavioural Ecology* (Ed. by J. R. Krebs & N. B. Davies), pp. 282–309. Oxford: Blackwell Scientific.

Dissanayake E (1999) ‘‘Making special’’: an undescribed human universal and the core of a behavior of art. In: Cooke B, Turner F (eds) Biopoetics. ICUS, Lexington, pp 27–46

Goldstein, R., Almenberg, J., Dreber, A., Emerson, J. W., Herschkowitsch, A., & Katz, J. (2008). Do More Expensive Wines Taste Better? Evidence from a Large Sample of Blind Tastings. *Journal of Wine Economics*, *3*(1), 1–9. doi:10.1017/S1931436100000523

Griffiths, P. (2014). Philosophy of Biology, *The Stanford Encyclopedia of Philosophy*, Edward N. Zalta (ed.), URL = <http://plato.stanford.edu/archives/win2014/entries/biology-philosophy/>.

Hansell, M.H. (2005) *Animal Architecture.* Oxford: Oxford University Press.

Hekkert, P., & van Wieringen, P. C. W. (1998). Assessment of aesthetic quality of artworks by expert observers: An empirical investigation of group decisions. *Poetics, 25*(5), 281-292.

Henrich, J. and McElreath, R. (2003). The evolution of cultural evolution. *Evolutionary Anthropology* 12: 123-135.

Hodgson, R. T. (2008). An examination of judge reliability at a major US wine competition. *Journal of Wine Economics*, *3*(02), 105-113.

Hodgson, R. T. (2009). An analysis of the concordance among 13 US wine competitions. *Journal of Wine Economics*, *4*(01), 1-9.

Johnstone, R. (2002). Signalling Theory: Signal Design and Selection for Efficient Displays, Coevolution Between Signaller and Receiver. In M. Pagel (Ed.), *Encyclopedia of Evolution*, Oxford University Press.

Kagan, J. (2009). *The three cultures: Natural sciences, social sciences, and the humanities in the 21st century*. Cambridge University Press.

Leder, H., Gerger, G., Dressler, S., & Schabmann, A. (2012). How art is appreciated. *Psychology of Aesthetics, Creativity, and the Arts, 6*(1), 2-10.

Miller, G. (2000). *The mating mind: How sexual choice shaped the evolution of human nature*. New York, NY: Penguin.

Mlodinow, L. (2009). A hint of hype, a taste of illusion. *The Wall Street Journal*.

Morrot G, Brochet F, Dubourdieu D (2001) The color of odors. Brain Language 79, 309–320

Odling-Smee, J. (2010). Niche inheritance. In: Pigliucci M, Müller GB (eds) *Evolution: the extended synthesis*. MIT Press, Cambridge, MA, pp. 175–207.

Odling-Smee, J., & Turner, S.J. (2012). Niche Construction Theory and Human Architecture. *Biological Theory*, 6, 283-289.

Pinker, S. (1997). *How the mind works*. Norton, New York

Powell, A., Shennan, S. and Thomas, M.G. (2009) Late Pleistocene demography and the appearance of modern human behavior. *Science* 324, 1298–1301.

Ramachandran, V. S., & Hirstein, W. (1999). The science of art: A neurological theory of aesthetic experience. *Journal of consciousness Studies*, *6*(6-7), 15-51.

Snow, C. P. (1959). *The two cultures and the scientific revolution*. Cambridge, England.

Sober, E. (2006). Parsimony. In: Sarkar, A. & Pfeifer, J. (eds.) The philosophy of science: an encyclopedia. Routledge, New York, pp 531–538

Sperber, D., & Hirschfeld, L. A. (2004). The cognitive foundations of cultural stability and diversity. Trends in Cognitive Science, 8, 40–46.

Spivey, N. (2005). How art made the world. BBC Books

Tooby, J., & Cosmides, L. (2001). Does beauty build adapted minds? toward an evolutionary theory of aesthetics, fiction and the arts. *SubStance* 30:6–27

Wolfe, T. (1975) *The Painted Word*. New York: Farrar, Straus & Giroux.

Part I

Chapter 1: Brian Boyd's Evolutionary Account Of Art: Fiction Or Future?

Introduction

Recently, there has been a surge in evolutionary approaches to art (e.g., Coe 2003; Boyd 2009; Dutton 2009). Here I discuss one such influential account, Brian Boyd's recent book, *On the Origin of Stories: Evolution, Cognition, and Fiction* (2009). The general aim of Boyd's work is to advocate evolutionary biology's relevance in understanding artistic achievements. This aim should be seen against the backdrop that many of Boyd's colleagues from the humanities (Boyd is Distinguished Professor of English at the University of Auckland and the world's foremost authority on the works of Vladimir Nabokov) are of the opinion that biology and evolution have no explanatory value for art whatsoever. Boyd develops his own evolutionary account of art in an attempt to demonstrate that the opposite is true. The essence of his thesis is that *art is an adaptation, biologically part of the human species, which derived–in the phylogenetic sense—from adaptive animal play behavior*.

I agree with Boyd that evolutionary biology can contribute to our understanding of art. Indeed, there is an increasing amount of research that unequivocally demonstrates this. However, I am worried about the specifics of the evolutionary account of art presented in the book. Basically, the arguments Boyd presents in defense of his view and the evidence he cites in support of them do not lead to the conclusion that art is a biological adaptation. Instead, I will argue, the evidence that Boyd provides in the book favors an alternative evolutionary view: *art as a cluster of culturally evolved practices*.

This chapter is structured as follows. In the next section, I briefly survey Boyd's exposition. I then evaluate Boyd's ideas, especially focusing on his arguments for art as a biological adaptation. I will argue why they do not hold in the light of current evidence, and propose instead that most of the arts evolved culturally, building on pre-existing biological traits.

Summary of Boyd's Account

A monumental work, at over 500 pages, the book is divided into two sections (''Book I'' and ''Book II'') of virtually equal length. The first part of the first section introduces the reader to some general concepts with regard to (human) evolution: human nature, adaptation, evolution of intelligence and of cooperation; all of which play an important role in Boyd's account. Part 2 offers an evolutionary account of art in general and Part 3 focuses on the evolution of fiction specifically. In the second section Boyd deals with two literary pieces, *the Odyssey* and *Dr. Seuss' Horton Hears a Who!*, which serve as test cases for Boyd's evolutionary literary criticism or ''evocriticism" based on the evolutionary analysis from the first half of the book. Boyd's evolutionary analysis of art is presented in Parts 2 and 3, therefore I will mainly focus on those parts.

In Part 2 Boyd presents his idea that art is phylogenetically derived from adaptive animal play behavior. (The idea is not original: it was developed earlier by Steen and Owens 2001, but Boyd does not cite them in his book.) Boyd claims that art has retained characteristics of ancestral nonhuman play but is also characterized by derived aspects that are unique to humans. The following are aspects that art retained from ancestral nonhuman animal play: Art is a practice in a safe context for behaviors that have key functions with regard to (adult) survival and reproduction; by repeatedly engaging in art, useful skills and relevant sensitivities that play a role in these adaptive behaviors are sharpened. This leads to measurable results on the neurological level: strengthened synaptic connections and brain growth (p. 191). Boyd calls this training of skills a ''major evolutionary function'' of art. In order to fulfill this function, art is highly self-rewarding—even compulsory—just as nonhuman mammalian play is, he argues.

But art also exhibits derived characteristics it does not share with play behavior in other animals, making it uniquely human. First, since ''humans gain most of [their] advantages from intelligence'' (p. 14), art is significantly more cognitive than non-human play behavior. In art, Boyd reasons, humans play cognitively with patterns of information that are humanly appropriate. Visual, aural, and social information are most relevant to human survival and reproduction, corresponding to visual art, music, and fiction, respectively. By compulsively playing with humanly appropriate patterns in art, humans strengthen the neural pathways that process these patterns. Second, art is also derived in that it acquired a suit of additional evolutionary functions. A first additional or ''subsidiary'' evolutionary function of art Boyd considers is social attunement: ''Art has played a key role in training and motivating us to share our attention in ever more finely-tuned forms'' (p. 101). Social attunement is beneficial because it enhances close cooperation. In music and dance humans may synchronize feeling and movement, and draw strength from this attunement. Visual art traditions such as in architecture, costume, hairstyles, etc., may signal and reinforce shared norms. Also fiction has this function, through stories that embody prosocial values (p. 106). A second subsidiary function Boyd envisions that art has is that it is a means for improving individual status. Boyd considers status enhancement a genuine evolutionary function of art. He suggests that being an artist enhances status and that in socially hierarchical groups, those of higher status have better access to resources and hence usually enjoy greater reproductive success. A final and ‘‘major’’ function Boyd proposes, gradually emerging out of the three previous functions (p. 119), is engendering creativity. Art generates a confidence that helps humans to modify the given in chosen ways, and it supplies them with skills and models that they can refine and recombine to ensure ongoing cumulative creativity. Boyd believes that, in evolutionary terms, ‘‘Nature has evolved art to create creativity’’ (p. 119) and ‘‘Art [is] effectively designed for creativity’’ (p. 121).

Part 3 is entirely devoted to fiction. Since Boyd considers fiction as an art, all aspects of art in general discussed in Part 2 apply to fiction as well and are explored in more detail in relation to fiction. Boyd explicitly distinguishes inventing stories from true narration. That humans are interested in the latter ‘‘poses no untoward biological challenge,” whereas humans’ interest in the pseudo-information of fiction poses an evolutionary puzzle: why do humans not prefer only true information, Boyd asks (p. 188). He suggests the answer lies in the fact that fiction as an art is an adaptation in its own right, that it is adaptive cognitive play with patterns of social information. Also in Part 3 Boyd presents a detailed developmental, cognitive, and comparative analysis of the components that constitute fiction. These components include Theory of Mind (ToM), systems for recalling, inventing and representing events, and so on. Much attention is paid to pretend play which develops early in human childhood and which may also occur in some nonhuman animals. Boyd considers pretend play to be where art ‘‘begins’’ (p. 96) and presents it as evidence for fiction as an innate adaptation. Further, Boyd discusses research that demonstrates that recalling events should be seen as reactivating past experiences and that the flexible recombination of these experiences allows humans to pre-simulate the future. The ‘‘prospective brain hypothesis’’ suggests that recalling the past and imagining the future even rely on the same cognitive mechanism; indeed, neurological research shows both activities involve the same brain regions (Schacter et al. 2007). These activities seem cognitively closely related to engaging in fiction. This has some interesting implications for explaining fiction (see below). Part 3 concludes with a discussion of fiction’s evolutionary functions (echoing the functions for art in general described above) and a discussion of evidence for fiction as adaptation. With respect to the latter, Boyd considers some evidentiary criteria for adaptation including ‘‘good design,’’ suggesting there is a tight fit between fiction and its evolutionary function. This and other evidence Boyd brings forward I will describe in more detail and evaluate in the next section.

Evaluating Arguments for Adaptation

Here I evaluate Boyd’s exposition, focusing on his argumentation for art as adaptation. I distinguish three main arguments. A first one is a cost-benefit thought experiment. The second argument is based on the view that art derived from adaptive animal play, acquiring additional evolutionary functions. Finally, Boyd applies some evidentiary criteria to art that are sometimes used in evolutionary psychology to demonstrate adaptation. I will argue that none of these arguments demonstrates that art is an adaptation.

A Thought Experiment

Boyd proposes to consider the thought experiment, ‘‘Nature selects against a cost without a benefit,” as an important piece of evidence for art as adaptation (p. 83). Boyd refers to the secondary loss of sight over evolutionary time in many burrowing or cave-dwelling animals as an example of this general principle. Sight is a costly ability and when redundant will be dispensed of by natural selection.[1] By analogy, Boyd notes, art is generally a costly activity in terms of time, energy, and resources devoted to it. He offers the following examples: Early visual art, such as scarification, tattooing, and body piercing, causes pain and risky injuries. Michelangelo spent years on his back painting the Sistine Chapel ceiling. More than a century of sponsorship has still not brought Gaudi’s design for Barcelona’s *Sagrada Familia* cathedral to completion. If there were no benefits attached to these costly artistic activities, the propensity to engage in them would have long been weeded out by natural selection. Therefore, Boyd concludes, art is evolutionarily functional and hence by definition an adaptation.

However, the problem is that Boyd has cherry-picked his examples here. First, with regard to costly art, his examples are all from the visual arts. A lot of visual art may be costly to produce but is the same true for fiction and music? Both these artistic activities do not necessarily require materials, in contrast to visual art. Fictional stories and song, for example, can be quite cheaply produced. Vocal chords and cognitive abilities are part of human biology anyway—i.e., maintained by selection for important functions in non-artistic activities (see below). Second, the comparison with selection for secondary loss of sight is also

[1] Note that selection against the cost of sight is just one possible explanation for the secondary loss of it. Neutral evolution by genetic drift is also considered a plausible explanation.

cherry-picked. The eye is an outlier in adaptations because it is a very specific organ that performs only one specific function. If the function of sight becomes redundant to a species, its eyes become redundant as well, and the selection pressure on functional eyes relaxes. But humans do not have an ‘‘art organ’’ that is specifically designed by natural selection for any biological function art may have. Instead, the ability to produce and experience art relies on a plethora of biological traits (cognitive, emotional, and motor) that all have functions in other contexts. Compare it to other things like ears and hands, which perform multiple functions. If one function of the human hand becomes redundant, it won't just disappear but it will be selectively maintained for the other functions it has. Therefore, for natural selection to weed out the human hand all functions for which it is under strong selection would have to have become redundant. The same is true for art. To weed out art, natural selection would have to select against at least one of the many biological traits art relies on. However, since each of these traits is also maintained by virtue of its vital functions in non-art contexts, this will not happen. Hence, natural selection cannot just weed out art's biological underpinnings because they are ‘‘constrained.’’ Therefore, the thought experiment is not a valid adaptationist test for art.

I stated there is no such thing as an art organ and explained why this is a problem for Boyd's account. The neuroscientific literature corroborates this. Boyd tends to treat art as a monolithic whole in his biological account of art, but this seems unwarranted since there is no biological ground to base this position on. There is no cognitive mechanism exclusively devoted to art. But even if the different arts are looked at separately, it becomes clear that humans do not possess a unitary cognitive ‘‘module’’ for any of them specifically. Let's take the three arts Boyd refers to in his thesis: visual art, music, and fiction. The evidence with regard to visual art is compelling. Half a century of neurological and neuropsychological research strongly suggests that visual art is a ‘‘multi-process activity,’’ i.e., depends on several brain regions and even on redundancy of art-related functional representation rather than on a single cerebral hemisphere, region, or neural pathway (Zaidel 2010). Boyd himself provides ample evidence that fiction involves both many different brain regions and cognitive mechanisms, and also that none of these mechanisms are exclusively devoted to fiction. Fiction relies on abilities such as a ToM, inventing, storing, and representing events, all of which are under comparably stronger selection for functions unrelated to fiction (see below). For music there seem to be some indications of the existence of music-specific cognitive specialization (Peretz 2006). Therefore, at present, music is an art form that has comparably most chances of eventually qualifying as adaptation. However, note that music also involves brain regions that have other tasks as well. For example, there is considerable overlap between brain regions involved in musical and linguistic tasks. As a result, even if further research would indicate that specific selection for musical abilities has occurred, it is still not justified to speak of a ‘‘music faculty’’ in the sense of a unitary module for music (Fitch 2006). Despite the indications of potential cognitive adaptation for music, the current evidence is not strong enough to refute the hypothesis that music evolved by piggy-backing on linguistic abilities, Fitch warns. Relevant to the problem with Boyd’s thought experiment he notes: ‘‘If music results automatically from linguistic mechanisms, then powerful selection for language could swamp weaker selection against music’’ (Fitch 2006, p. 200).

Multifunctional Playground

Boyd’s second set of arguments for adaptation is based on his view that art is a phylogenetically derived form of adaptive animal play that acquired additional evolutionary functions. Adaptations have, by definition, evolutionary functions. Therefore, demonstrating function is demonstrating adaptation. In the previous section I already summarized the four evolutionary functions Boyd claims art has. Here I will evaluate the evidence for these claims and I will conclude that at present it does not allow us to claim adaptation for any evolutionary function. In addition, Boyd assumes that if art derived from adaptive animal play it must be adaptive itself. However, this is not necessarily the case. I will start off with evaluating this assumption.

The problem with Boyd’s assumption that if non-human animal play is adaptive, human art, a form of play in Boyd’s view, must be adaptive as well is that an adaptive explanation of a behavior does not necessarily explain all instances of that behavior. Take as an example the socially transmitted behavior of the seemingly purposeless stone handling by *Macaca fuscata* (Japanese macaque), which may involve devoting large amounts of time and effort to collecting, rubbing, clacking together, scattering, and regrouping stones, observed in provisioned and captive troops in Japan. Although stone handling may have emerged from an adaptive tendency to play in these animals, it is in itself nonadaptive. Over 30 years of research on this behavior has yielded no evidence of an evolutionary function of the behavior itself (Huffman 1984; Huffman et al. 2008). It cannot be considered as a practice for useful behaviors (these animals are not tool users). It is rather considered a nonfunctional solitary object-play activity that results from a self-rewarding physiological predisposition probably linked to foraging behavior (Huffman and Quiatt 1986). Interestingly, despite the lack of an ultimate evolutionary function, the proximate mechanism of being selfrewarding drove its rapid spread and persistence over these populations of socially interacting macaques. In the same sense, regardless of the unequivocal importance of play in human development, in so far as art qualifies as adult play, it may just as well be a culturally maintained unselected by-product of the human tendency to play instead of an adaptive practice for human functional behavior. To be sure, Boyd does not deny culture plays a role in art and he devotes quite some attention to ''biocultural'' aspects of artistic behavior. However, he lumps organic evolution and cultural evolution together: ''I … use 'biocultural' and 'evolutionary' almost interchangeably'' (p. 25). Yet, the above example illustrates that a biologically inherited behavioral predisposition that may be an adaptation for a function can become co-opted in a culturally evolved practice in which it does not serve that function. Moreover, whether the culturally evolved practice is adaptive or not does not depend on whether the biological traits it co-opts are.[2] Before taking a look at the evidence for the evolutionary functions of art Boyd proposes, it is important to consider the following caution. Demonstrating that a trait is evolutionarily beneficial (i.e., increasing reproductive success) by itself is insufficient to demonstrate adaptation. The notions of adaptation and evolutionary function are inextricably linked. An evolutionary function is a beneficial effect of a biological trait for which that trait underwent selection, for which it was modified or ''designed'' by natural selection. Therefore, if it can be demonstrated that art has a beneficial effect, it is an indication for art as adaptation. However it cannot by itself be regarded as solid proof because a trait can be beneficial without having been selected for it, a phenomenon called exaptation (Gould and Vrba 1982; Gould 1991).[3] For example, most humans today can write and read without ever having been selected for these tasks. Latent abilities like these are also found in other animals. For example, orangutans are skillful tool users in captivity but, notwithstanding an interesting exception, orangutan populations do not exhibit tool use in the wild (van Schaik 2006). Thus, even if future research were to demonstrate that art has certain beneficial effects to those engaging in it, this is not in itself evidence for art as adaptation. This caveat notwithstanding, finding evidence of beneficial effects of art is a required step to demonstrate adaptation. Since, as discussed above, the biology of art cannot be treated as a monolithic whole, the arts Boyd discusses—fiction, music, and visual art—must be considered separately.

With regard to the first beneficial effect of art Boyd proposes, the training of cognitive skills, Boyd does not supply any evidence that points to such an effect. The reason may be that studies have yet to be conducted testing this hypothesis. It is a research area still in its infancy. Also, Boyd does not distinguish

[2] Also see the review by Mellmann (2010) who came to similar conclusions with regard to Boyd's account and the role of culture in the evolution of art.
[3] ''Beneficial'' suggests that reproductive success is positively influenced and as a result the gene frequency for the trait in the population may increase. However, since the trait itself is not modified, it is unwarranted to speak of selection in this context (Andrews et al. 2002).

between production of art and consumption of art with respect to this function. However, it seems likely that if art trains skills that are valuable outside the art context it will above all be art production—which is much more intense as a practice than consumption—that will have that effect. For example, there is recent evidence that *intensive* music training may tone the brain for auditory fitness (Kraus and Chandrasekaran 2010). Listening by itself, on the other hand, is not sufficient, research suggests. A well-known example of overhyping the latter effect is the so-called Mozart effect, the hypothesis that listening to classical music enhances spatial intelligence, which even spawned a small industry. However, regardless of the many attempts to show such an effect exists, a meta-analysis of 16 studies demonstrated that there is no such effect (Chabris 1999). With regard to fiction there are some correlational studies that explored possible positive effects of engaging in fiction (reading fiction, acting classes, etc.) on the development of ToM and empathy. Results for empathy are mixed, but for ToM there may be some evidence of a reciprocal relationship (Goldstein and Winner 2012). However, as the authors note, the studies that demonstrated correlation were not designed to conclude anything with respect to causation; it could well be that subjects that were more inclined to read a lot of fiction or motivated to take acting classes possessed a more developed ToM in the first place.

Second, there is the idea that art contributes to social attunement of individuals favoring the beneficial behavior of close cooperation. With regard to music Boyd refers to a recent study that showed that singing lowers men's testosterone levels, indicating, Boyd believes, that music may contribute to cooperation rather than competition. Further Boyd quotes some authors suggesting that human societies use synchronized movement to create harmony and cohesion within groups. Boyd notes that visual art serves to reinforce shared norms, but he does not refer to any studies corroborating this. Similarly he suggests that fiction may stimulate the adoption of prosocial values but cites no evidence. There is a need for experimental and systematic observational studies to explore whether or not such effects exist.

A third evolutionary function of art Boyd suggests is improvement or maintenance of an individual's social status in a group. However it is not clear from Boyd's account how the function of enhancing status could have exerted a selective pressure on art. Boyd notes that modern hunter-gatherer societies are generally egalitarian; attempts by individuals to enhance their status are thwarted by mechanisms such as ridicule, ostracism, and even expulsion. Only in societies with agriculture can surpluses be hoarded and disparities grow, allowing status enhancement, Boyd notes. This is problematic. Admittedly, the social structure of modern hunter-gatherer societies cannot just be extrapolated to human prehistoric societies. Nonetheless, it is more plausible that prehistoric societies were more similar to modern hunter-gatherer societies than to the relatively recent agricultural societies. Taking this into account, the function of status enhancement must be very recent (and if it occurred, limited to post-agricultural peoples) and therefore unlikely to have exerted any significant selection pressure on art.

Finally there is the proposal that art is a system for engendering creativity. Boyd claims that, ''Nature has evolved art to create creativity'' (p. 119) and ''Art [is] effectively designed for creativity'' (p. 121). Thus implied is that creating creativity should be considered as a genuine evolutionary function of art. Yet, elsewhere Boyd proposes that this function gradually emerges out of the three previous functions (p. 119). And indeed Boyd seems to assume creativity is a very recent function of art when he notes that there are ''changing functions of art in more modern times, its increasing association with creativity and innovation rather than with conformity and tradition" (p. 114). Be that as it may, Boyd does not discuss any evidence for either general creativity emerging from engaging in art nor studies that show that creativity itself pays off in terms of fitness.

Of course Boyd cannot account for the current lack of evidence of beneficial effects of the arts, and the limited explanatory power with regard to adaptation any evidence that eventually may be found would have. But this brief evaluation of potential beneficial effects of the arts does point out that it is currently unwarranted to claim that any of these arts is adapted to any of these effects. As Williams (1966) warns in his seminal work on natural selection: demonstrating adaptation carries an onerous burden of proof. Moreover, he says, ''[adaptation] should be used only as a last resort'' (Williams 1966, p. 11). And Boyd's account does not convince that adaptation is the only option left to explain the evolution of art.

Evidentiary Criteria

Boyd discusses three evidentiary criteria that are generally used in evolutionary psychology to demonstrate cognitive adaptation for an evolutionary function: (1) good design or tight fit, (2) universality, and (3) developmental reliability of a trait. However, as I will argue, these criteria do not allow alternatives to art as adaptation to be refuted either.

Throughout his exposition of the evolution of art Boyd regularly refers to the argument of ''good design" in order to demonstrate adaptation. The idea of good design is that, as a result of natural selection, the features of an adaptation will often be tightly fit to that adaptation's function (Cosmides and Tooby 1995). For example, there is a tight fit between the features of the eye and its function of sight. Boyd expands on this evolutionary standard with regard to fiction specifically. In his discussion of fiction as adaptation Boyd claims to ''have explained the design for fiction'' (p. 190). He refers here to the extensive account he offers of systems of event comprehension, representation and storage, theory of things, kinds, and minds, joint attention, and the reliable emergence of pretend play. Boyd indeed convincingly demonstrates a tight fit between fiction on the one hand and these cognitive capacities on the other hand. But clearly, Boyd wouldn't argue that these capacities evolved *for* fiction—or more correctly for fiction's function(s). Yet, the latter is exactly what he would need to demonstrate in defense of his view that fiction is an adaptation. The mere observation that fiction may involve cognitive adaptations is no proof of fiction as adaptation whatsoever. Indeed, good design is not only consistent with adaptation but also with alternative explanations. The tight fit between fiction and its underlying cognitive components can just as well result from fiction—as a culturally evolving practice—adapting to human cognition. Indeed as Boyd (p. 64) himself notes (contradicting his main argument):

> Stories arose…out of our intense interest in social monitoring. They succeed by riveting our attention to social information, whether in the form of gossip…or fiction.

But again: that human interest in social monitoring is adaptive by no means demonstrates that fictional stories that appeal to that interest are adaptive as well. This is a frequently recurring misunderstanding in Boyd's account. With regard to the capacity to invent fictional stories Boyd refers to compelling neuroscientific research. The prospective brain hypothesis suggests that memory and prospect are relying on the same cognitive mechanism (Schacter et al. 2007). Indeed, studies show that imagining the future depends on much of the same neural machinery that is needed for remembering the past: brain regions that have traditionally been associated with memory appear to be similarly engaged when people imagine future experiences. Instead of passively recording, human memory reactivates, almost simulates, prior experiences. This in turn allows recombining freely past experience so that the individual can imagine or pre-simulate the future. Episodic memory in particular is crucially involved in the ability to simulate future happenings. In addition, the same mechanisms may allow exploring the results of different possible actions (for example: I wonder what will happen if I try to steal their food?). Importantly, from this perspective on imaginative capacity it follows that cognitively there is no distinction between creating fiction, i.e., inventing stories, and predicting the future. Inventing stories relies equally on this neural machinery of the prospective brain as contemplating a prospect does. (An interesting test would be to check, as expected from this view, whether the same brain regions are indeed involved in fiction.) However, when it comes to evolutionary function there has to be quite a significant difference. A capacity for imagining the future or potential actions obviously implies strong, direct benefits. By contrast, even if the art of fiction would prove to be evolutionarily beneficial, the selection pressure resulting from such benefits would be negligibly weak in comparison. Therefore, the hypothesis that fiction is a culturally evolved by-product that piggy-backs on the crucial function of the prospective brain seems favorable.

Universality of a trait is another evidentiary criterion Boyd regularly appeals to. Art occurs virtually universally across human peoples and cultures. Boyd considers this as an indication that art is not purely cultural. However, the ability to read also comes close to being a human universal. Yet, evolutionary psychology wouldn't state that humans have a ''reading instinct'' (Changizi 2011). Hence, universality is also consistent with culturally evolved practices. Of course art is much older than reading (at least traditional arts are), but being old is by itself no indication of biological adaptation either.

Finally Boyd discusses the evolutionary criterion called reliability of development. Boyd devotes quite some attention to the argument that fiction develops reliably and spontaneously (without training) in early childhood in the form of pretend play. Boyd notes that infants from a year, a year and a half, start manipulating objects as if they were something else. A classic example is the pretend play with cup and teapot. A cup that has been pretend-filled by a pretend-pour from an actually empty teapot will spill its pretend contents if knocked over, and children will refill only the ''spilled'' cup, not the others, even if all are in fact empty. Although I agree that pretend play offers a fascinating view on the development of capacities required for fiction, I have two concerns with regard to the statement that pretend play accounts as evidence for fiction as adaptation. A first concern regards the relation between children's pretend play and the art of fiction. Boyd himself acknowledges that, ''We would not call pretend play art" (p. 5); rather Boyd considers pretend play is where art ''begins'' (p. 96). Therefore even if pretend play were a reliably developing adaptation, it by itself does not mean fiction is an adaptation. The alternative that the art of fiction is a culturally maintained by-product of adaptive pretend play would also be consistent with that finding. A second concern is that pretend play may not even qualify as an adaptation itself. The criterion of reliability of development is similar to the previous one in that it appeals to universality, only this time on the developmental level. With regard to pretend play it may also suffer from the same problem. That is, reliable development of pretense in childhood (or what adults perceive as pretense) may be due to cultural induction instead of innate mechanisms. At least that is what recent studies indicate (Rakoczy et al. 2005). For example Striano et al. (2001) found that before 2 years of age, young children's pretense with objects derived almost exclusively from imitation of adults or from adult verbal instructions sometimes with acting on toys with established pretense functions. This puts the cup and teapot example in a different light: children may be taught to pretend play with the objects. The authors claim that if 2-year-old children were not exposed to other persons pretending, they would not invent pretense for themselves as a solitary activity at this young age. Hence, these studies suggest that pretend play is a culturally learned practice. Of course, this is not to say that the practice of pretend play may not also rely on automatic cognitive tendencies of children, but we would not call pretend play, as a trait, an innate adaptation.

Conclusions

By providing fascinating examples (e.g., elaborate bubble play in dolphins) and a broadly sweeping and very informative discussion of relevant theories and findings from a multitude of research disciplines (i.e., philosophy of art and art criticism, anthropology, evolutionary and developmental psychology, ethology, and neurobiology), Boyd succeeds in making the reader enthusiastic about art and the insights and lines of thinking an evolutionary approach to art can yield. For this Boyd's monumental effort is to be applauded, the more so as to date few books exist devoted specifically to the evolution of art. Unfortunately, however, as I have discussed at length, the book suffers from weak and at times inconsistent evolutionary argumentation, which tempers my enthusiasm. Particularly, Boyd's arguments for art as a biological adaptation are unwarranted. Reviewing Boyd's evolutionary thesis I have formulated three main concerns. One was on the level of evolutionary effect. I formulated two reasons why Boyd's claim that art has evolutionary functions is presently unwarranted. First, it cannot be concluded from the evidence Boyd provides that any of the arts discussed evolved because it enhanced reproductive success of its producers or experiencers. Second, even if it were to be demonstrated that some form of art has some beneficial effect, it would not necessarily mean that this effect is an evolutionary function, i.e., that the biology underlying art was selectively altered for it. Art exapted to that beneficial effect, i.e., without undergoing selection for it, would also be consistent with it. Yet, Boyd does not devote any space to discussing this alternative. There is in fact cause to assume that exaptation would be an at least as plausible explanation in such a case as adaptation. This relates to the second concern I expressed with respect to Boyd's account, which is on the level of trait. Boyd claims that there is evidence for cognitive adaptation for art. This is however not supported by neurobiological evidence. With the exception perhaps of music, no biological (i.e., cognitive) adaptation for any of the arts, and definitely not for art in general, seems to have occurred. Each art form involves several cognitive mechanisms and brain regions under selection pressure for crucial non-art functions instead of one devoted ''faculty.'' Therefore, if fiction or visual art prove to be beneficial, the conclusion that they are exapted to that effect, instead of adapted, may be favored at this point. My final concern relates to the fact that Boyd explicitly lumps together organic and cultural evolution without providing a consistent argumentation why this simplification would be justified. Throughout my evaluation of the book I have hinted at a possible alternative evolutionary perspective on the arts that does take into account the distinction between organically and culturally inherited traits: the arts as culturally evolved practices. Perhaps, art thus can be seen as a cluster of culturally evolved practices, rather than a biologically evolved monolithic whole. This is not to say that biology plays no role in art. On the contrary, the point is that art has evolved culturally adapting itself to the pre-existing biological traits on which it relies. Thus, I propose explaining the tight fit between art and cognition the other way around from Boyd: art has been culturally selected to fit human cognition.

My aim was not to argue against an adaptationist approach to the arts. To the contrary, I concur with Boyd that adaptationism, accommodating recent cross-disciplinary findings, can yield interesting research questions and hypotheses about the arts. However, taking cultural transmission as a partly independent process from biological evolution and a comparative evaluation of adaptation and alternatives seriously is paramount for developing a sound evolutionary research program of art.

Acknowledgments

Thanks to Brian Boyd for discussion of the book, and Wayne Christensen, Rachael Brown, Brett Calcott, and Eran Shifferman for commenting on an earlier version of this manuscript. This paper was supported by the Research Foundation— Flanders (FWO) and the Konrad Lorenz Institute for Evolution and Cognition Research, Austria.

References

Andrews P, Gangestad S, Matthews D (2002) Adaptationism: how to carry out an exaptationist program. Behav Brain Sci 25:489–553

Boyd B (2009) On the origin of stories: evolution, cognition and fiction. Belknap Press of Harvard niversity Press, Cambridge

Chabris CF (1999) Prelude or requiem for the ''Mozart effect''? Nature 400:826–827

Changizi M (2011) Harnessed: how language and music mimicked nature and transformed ape to man. Benbella Books, Dallas

Coe K (2003) The ancestress hypothesis: visual art as adaptation. Rutgers University Press, New Brunswick

Cosmides L, Tooby J (1995) Beyond intuition and instinct blindness: toward an evolutionarily rigorous cognitive science. Cognition 50:41–77

Dutton D (2009) The art instinct: beauty, pleasure and human evolution. Oxford University Press, Oxford

Fitch WT (2006) The biology and evolution of music: a comparative perspective. Cognition 100:173–215

Goldstein T, Winner E (2012) Enhancing empathy and theory of mind. J Cogn Dev 13:19–37

Gould SJ (1991) Exaptation: a crucial tool for an evolutionary psychology. JSI 47:43–65

Gould SJ, Vrba ES (1982) Exaptation: a missing term in the science of form. Paleobiology 8:4–15

Huffman MA (1984) Stone play of *Macaca fuscata* in Arashiyama B troop: transmission of a non-adaptive behavior. J Hum Evol 13:725–735

Huffman MA, Quiatt D (1986) Stone handling by Japanese macaques (*Macaca fuscata*): implications for tool use of stone. Primates 27:413–423

Huffman MA, Nahallage CAD, Leca J (2008) Cultured monkeys: social learning cast in stones. Curr Dir Psychol Sci 17:410–414

Kraus N, Chandrasekaran B (2010) Music training for the development of auditory skills. Nat Rev Neurosci 11:599–605

Mellmann K (2010) The multifunctionality of idle afternoons: art and fiction in Boyd's vision of evolution [review of Brian Boyd, On the origin of stories: evolution, cognition, and fiction, 2009]. JLT Online Reviews. http://www.jltonline.de/index.php/reviews/article/ view/170/530. Accessed 26 March 2012

Peretz I (2006) The nature of music from a biological perspective. Cognition 100:1–32

Rakoczy H, Tomasello M, Striano T (2005) On tools and toys: how children learn to act on and pretend with ''virgin objects.''. Dev Sci 8:57–73

Schacter DL, Addis DR, Buckner RL (2007) The prospective brain: remembering the past to imagine the future. Nat Rev Neurosci 8:657–661

Steen F, Owens S (2001) Evolution's pedagogy: an adaptationist model of pretense and entertainment. J Cogn Cult 1:289–321

Striano T, Tomasello M, Rochat P (2001) Social and object support for early symbolic play. Dev Sci 4:442–455

van Schaik C (2006) Why are some animals so smart? Sci Am 294(4):64–71

Williams GC (1966) Adaptation and natural selection. Princeton University Press, Princeton

Zaidel D (2010) Art and brain: insights from neuropsychology, biology and evolution. J Anat 216:177–183

Chapter 2: Extending Literary Darwinism - Culture And Alternatives To Adaptation

Introduction

"Literary Darwinism" seeks to explain such human behaviors and achievements as storytelling, fiction and literature (referred to here as "literary behaviors") from a Darwinian perspective, and this is no doubt a useful endeavor. There is an in- creasing amount of research that unequivocally demonstrates that an evolutionary approach can contribute to our understanding of human behavioral phenomena, including artistic production and appreciation.

However, some scholars within this field seem to consider evolutionary theory as a rough-and-ready manual that enables explaining ad hoc any aspect of human behavior of interest. Yet, although evolutionists agree about the basics of the theory, evolutionary theory itself continuously evolves. Rather than being an explanatory automaton, as it is sometimes naively regarded and applied, it is a research program in progress.

Here I wish to discuss two problems surrounding an evolutionary approach to literary behaviors. First, there is the question of adaptation. The problem is not so much — or not only — the question of whether a given literary behavior is an adaptation, but rather whether some accounts lack in scientific rigor when evaluating that hypothesis. For instance, the term "adaptive" is often treated in these accounts as synonymous with "evolutionarily beneficial" while it is important to distinguish between these two concepts. Moreover, assessing whether a trait is an adaptation requires comparatively evaluating and scrutinizing one by one alternatives to the adaption explanation. Second, the role culture plays in literary behaviors is not straightforward and requires special attention. Many accounts in Literary Darwinism rely heavily on standard evolutionary psychology (EP). It is beyond doubt that the EP-approach to literary behaviors has spawned interesting insights, hypotheses and avenues of empirical research. However, EP is just one school of thought studying behavior from an evolutionary perspective — with specific explanatory focus and assumptions. Standard EP often treats culture either as a factor we can leave out of the evolutionary equation or as a simple functional extension of genetic evolution (Dutton, 2009; Boyd, 2009; Lumsden & Wilson, 1981; Wilson, 1999; Cosmides & Tooby, 1989). Yet, there is increasing theoretical and empirical evidence that culture should be treated as an inheritance system that evolves partly independent from genetic evolution and, moreover, which may af- fect genetic evolution. This body of work is termed “Gene-Culture Coevolution” or “Dual Inheritance” (Boyd & Richerson 1985; Richerson & Boyd 2005). The cultural evolution approach to fiction, for example, allows formulating a plausible alterna-tive view to the one exclusively based in standard evolutionary psychology: literary behaviors as culturally evolved practices building on pre-existing biological traits.

Adaptationism

An adaptation in biology is a trait with a current functional role in the life history of an organism that is maintained and evolved by means of natural selection. An adaptation refers to both the current state of being adapted and to the evolution- ary process that leads to the adaptation. Simply put, an adaptation is a trait that is selectively altered for the beneficial effect that trait has. For example, the eye clearly contributes to survival of an organism as a means to effectively assess its environment, and eyes have been modified by selection for the perceptive role they have. They did not evolve in their entirety for some other function. Adaptationism is a research program, quite central to evolutionary study, which is devoted to testing whether a particular feature of an organism qualifies as adaptation.

In line with this, the first — and sometimes the only — question many Literary Darwinists ask is what the adaptive value or adaptive significance is of fiction, storytelling, and literature (see the writings on this topic by, among others, Brian Boyd, Dennis Dutton, Leda Cosmides and John Tooby, Joseph Carroll, Eduard O. Wilson, Geoffrey Miller, Ellen Dissanayake).They argue, for instance, that a number of criteria for demonstrating adaptation are met. One procedure often appealed to is a cost benefit analysis, claiming that the evolutionary benefits of a literary behavior outweigh its costs. Another claim is that a given literary behavior is universal among humans, that it develops reliably and spontaneously in children, that the literary behavior involves innate dispositions, and that there is a tight fit between the substrate of the behavior (the cognitive device) and its behavioral output. It is often argued that these conditions are all met and that they — taken together — suffice for demonstrating adaptation. A more careful analysis, however, shows that this is not the case. The problem is that these conditions alone — even when they are fulfilled — do not allow refuting certain alternatives to adaptation. Careful adaptationists commit to a procedure that overcomes this problem. Or as Williams (1966) put it in his seminal account on natural selection: “[adaptation] should be used only as a last resort” (Williams, 1966, p. 11). The idea is that we should only make an inference of adaptation after demonstrating that all alternative hypotheses to adaptation for a particular effect are highly unlikely as complete explanations for the trait. Fortunately, Literary Darwinists do sometimes consider alternatives to adaptation. But unfortunately, they usually only consider one, which is the by- product hypothesis. The by-product hypothesis states that a given trait did not evolve because it was selectively advantageous, but because it was a byproduct of selection for another trait. Yet, there are other alternatives to adaptation that need to be scrutinized before turning to adaptation. The two most important alternatives, next to by-products, are “constraint” and “exaptation” (see below). It seems that these alternatives are especially ignored in evolutionary psychology (more so than in evolutionary biology). The reason may be a historical rather than a scientific one: the foremost advocate of a careful adaptationism, the late palaeobiologist Stephen Jay Gould, made himself unpopular with a rather direct attack on those he called “pan-adaptationists”, evolutionists who hold the idea that virtually all of the characteristics of living organisms are adaptations. This is not the place to go into the details of this clash of evolutionists. I just mention this because a lot of evolutionary psychologists threw the baby out with the bathwater. As Williams (who is, contrary to Gould, not controversial at all) already stressed, considering alternatives to adaptation is paramount to a science of evolution. I will now discuss these three alternative evolutionary explanations in the context of literary behavior.

Exaptation and constraint

Remember that an adaptation is a trait that is selectively altered for the beneficial effect that trait has. In such a case the effect of the trait is called an evolutionary function. Adaptations thus have, by definition, evolutionary functions. But a trait may also have a beneficial effect for which it was not selected. In that case it qualifies as an exaptation. Thus, an exaptation is a pre-existing trait (i.e., one that has already evolved) that acquires a new beneficial effect without being modified by selection for this effect (i.e., it takes on a new role, but was not designed for it by selection) (Gould & Vrba, 1982; Gould, 1991). Crucially, although not always appreciated (which may explain the neglect), the new fitness enhancing effect is acquired without subsequent phenotypical modification by selection for the effect (Andrews et al., 2002). Take, for example, the ability to read and write or to drive a car, which are all part of the behavioral phenotype of many contemporary humans. These behaviors have obvious current utility but the cognitive mechanisms on which they rely were not selectively altered for that utility. They build on pre-existing biological traits. If a prehistoric Homo sapiens would be teleported to our time, she would be able to acquire all these capabilities just as we have learned them through social learning.

Taking exaptation seriously, it follows that we need to reconsider the validity of some of the central criteria for adaptation summed up above. First, consider the cost benefit analysis. Although quite hard to measure empirically, it may be demonstrated that a given literary behavior entails a net benefit. For example, an intensive course in novel writing may pay off in terms of increased social intelligence, with measurable neural growth in the areas involved in empathy and theory of mind. Moreover, it may be demonstrated that increased social intelligence also enhances survival and reproduction (otherwise natural selection cannot act on it). Thus, in this hypothetical example, novel writing is genuinely evolutionarily beneficial, which excludes the by-product hypothesis because the latter entails that novel writing does not have a beneficial effect. That would leave us with exaptation and adaptation, which both require the trait to be evolutionarily beneficial. Unfortunately, the hypothetical findings on novel writing do not allow us to refute exaptation. In order to do that, we would need to demonstrate that the biological traits underlying novel writing were selectively altered for the purported beneficial effect. Since writing is likely a culturally evolved trait that relies on pre-existing biological (i.e., cognitive and motor) traits, novel writing quite likely is too. Therefore the cost benefit analysis by itself does not demonstrate adaptation.

The evolutionary concept of constraints is relevant as well and entails an alternative that needs to be considered before moving on to claims of adaptation. A constraint opposes the modifying influence of selection on the phenotype. This concept seems especially relevant to testing evolutionary hypotheses of literary behaviors because these behaviors typically rely on a number of biologically inherited traits that serve important roles in other contexts. Or, in other words, scientists haven't been able to find any biologically inherited traits that are exclusively (nor especially) devoted to literary behavior. Storytelling, fiction and literature use cognitive capacities that are used in "real life" as well, such as the ability to track agents, to share attention, to hold mental representations in the mind and to evaluate scenario's for future actions, and so on. In fact, all cognitive traits literary behaviors rely on have quite vital roles for which they are under strong selection pressure. Clearly, this puts a strong constraint on any of the traits upon which literary behavior rests. Therefore, we can conclude that selection cannot operate on these biological traits for any beneficial effect literary behavior may have (a precondition for adaptation). Thus, the concept of constraint further adds to the picture that literary behaviors unlikely qualify as biological adaptations.

The second conjecture Literary Darwinists appeal to, namely, that given that a literary behavior involves innate dispositions counting as evidence for literary behavior being an adaptation is not valid either. Involvement of innate dispositions in a behavior does not allow refuting any of the alternatives to adaptation. Even a by-product may involve innate dispositions. As long as it is not demonstrated that any of these innate dispositions have been selectively altered for a beneficial effect of literary behavior, it does not qualify as adaptation. For this reason, concepts such as the "art instinct" are somewhat problematic. As Dutton argues (following E. O. Wilson), the arts "extend" evolved traits. But either we consider them as being integral parts of the traits they are extensions of (and in that case, the term art instinct is misleading because it suggests a separate category that is biologically meaningful) or we do consider the arts as separate from the traits they are extensions of, but in that case the biologically inherited traits on which they rely have to have been selectively modified for the beneficial effects a given art practice may have, and as I pointed out above, there is virtually no support for this claim. The other commonly referred to evolutionary criteria, universality and reliability of development, need to be reconsidered in the context of cultural evolution, which is the topic of the next section.

Cultural evolution

Cultural inheritance is regarded as an inheritance system similar enough to genetic inheritance to be considered as evolving in a Darwinian fashion (i.e., selection pressures acting on cultural variants). Cultural variants (such as ideas, opinions, values, behaviors, etc.) that are acquired through social learning often cannot be considered as extensions of genes. Evolutionists have demonstrated theoretically and empirically that cultural and genetic evolution sometimes operate independently and even antagonistically. For example, selection may favor academics who produce papers, increasing their "cultural fitness" at a cost of their "biological fitness", i.e., producing babies (Richerson & Boyd, 2005). Thus cultural evolution may lead to behaviors that are maladaptive from the perspective of genes. Dual Inheritance or Gene-Culture Coevolution allows investigating the relative roles of cultural and genetic inheritance from a Darwinian perspective.

Taking cultural evolution seriously is necessary to address the evolution of literary behaviors. Consider the following example. Disgust, which is comprised of a diverse but highly coordinated set of elements, including affective, behavioral, and cognitive components, initially evolved to monitor food intake and protect against parasites and pathogens (Ekman, 1992; Rozin et al., 2008). However, in humans many other additional stimuli may elicit disgust, including a certain class of social norms called purity norms (Kelly, in press). Now, research has shown that urban legends in part succeed on the basis of emotional selection, for example, the ability to evoke disgust: Heath and Sternberg (2001) demonstrated that people are more willing to pass along stories that elicit stronger disgust or versions of stories that elicit the highest level of disgust. Obviously, the fact that a disgust response influences the success of urban legends is an evolutionary side effect and not an extension of its evolved function. Urban legends exploit the human disgust response in order to spread; in that sense they are what Dawkins (1976) dubbed "memes", parasitic pieces of culture rather than functional extensions. The same seems to be true of romantic novels that capture their audience in virtue of eliciting negative emotions. Consider the reported gulf of "copycat" suicides following the publication of Goethe's *Die Leiden des jungen Werther* (The Sorrows of Young Werther). Negative emotions, such as fear, anger and disgust are just much more evoluti onarily relevant than positive ones. Often they require immediate action in order to survive. Therefore, they elicit a problem-solving attitude in experiencers (they make you think), heightened attention and memory. Consequently, it is easy to see why they play such a prominent role in the evolution of literary behavior. To be sure, Literary Darwinists sometimes do incorporate social learning and cultural transmission into their accounts. However, in doing so, they rarely — if at all — consider how cultural evolution may deviate behavior from what would be expected on the basis of genetic evolution as just described. For example, Boyd (2009, p. 25) writes: ''I ... use 'biocultural' and 'evolutionary' almost interchangeably,'' lumping genetic and cultural evolution explicitly together. Yet the example above of disgust illustrates that a biologically inherited predisposition, which is an adaptation for a function, can become co-opted in a culturally evolved practice in which it does not serve that function (Sperber & Hirschfeld, 2004). Thus, my point here is that cultural content often exploits responses of human evolved psychology for which they didn't evolve.

Literary Darwinists and other evolutionists of human behavior sometimes treat universality of a trait as evidence that the trait is a biological adaptation. The idea is that natural selection would weed out any evolved traits that are incidentally maladaptive. Therefore, a maladaptive trait that is universal among humans and relatively old would surely not persist. However, the above example of negative emotional selection already contradicts this assumption. Moreover, a trait may even be evolutionarily beneficial and universal and nonetheless not a biological adaptation. Take the example of the ability to read and write again. Reading comes close to be a human universal nowadays (world literacy is currently nearing 90% according to UNESCO (i.e., some 776 million adults lack minimum literacy skills)) but we wouldn't claim humans have a reading instinct. Evolution has no foresight, our ancestors did not evolve cognition to allow us at some point in time to be able to read. Therefore universality is not a valid criterion for demonstrating adaptation. The penultimate evolutionary criterion I wish to address here is reliability of development. Sometimes evolutionary psychologists claim that if a cognitive trait develops reliably and spontaneously early in childhood this is an indication that it qualifies as an innate adaptation coming to expression. For example, some authors have linked the early emergence of pretense and pretend play in infants to fiction, arguing that pretend play is a beginning phase of a capacity for fiction (e.g., Boyd, 2009). However, much recent research in developmental psychology demonstrates the importance of social learning from a very young age on. Studies suggest that pretend play, rather than being a spontaneously developing innate adaptation, in fact results from copying parents (a child perceives its parents filling a cup with a teapot and feels the urge to do the same, regardless of whether the cup and teapot are toys that contain no tea) (Rakoczy et al., 2005; Striano et al., 2001). Cross- cultural evidence might further corroborate these findings. For example, in Mali, children in savannah villages do not know to play (pers. comm. Willie Van Peer). Finally, there is the criterion of special design, that there exists a tight fit be - tween the behavior (with its alleged evolutionary function) and the biological substrate that produces it. For example, the eye is so well designed for the function of visual perception that it seems quite unlikely that it evolved for another function. Literary behavior also exhibits this tight fit with human cognition. This is demonstrated by the fact that people sometimes compulsively engage in fiction. But given the considerations above, namely that literary behaviors rest on cognitive traits that were selected in other, real life, contexts, it seems reasonable to explain the tight fit between human cognition and fiction, the other way around from how Literary Darwinists explain it: fiction evolved by culturally adapting itself to human cognition. In fact for example Boyd (2009, p. 64) makes this claim himself when he contends that fictional "stories arose out of our interest in social monitoring," in so doing inadvertently contradicting his own view of fiction as adaptation.

Conclusion

First, I argued that claims of literary behaviors being biological adaptations on their own are theoretically and empirically weak (and even unsound) and reliant on shaky evolutionary standards. As yet we are not in a position to draw such conclusions. Researchers should take the alternatives to adaptation more seriously. Moreover, they should not only weigh adaptation against the by-product hypothesis, but also take exaptation and constraint into consideration. With respect to function it is important to distinguish between "evolutionary function" and "evolutionarily beneficial effect", the former being a specific type of the latter.

Second, I advocated that the standard evolutionary psychology approach Literary Darwinists usually apply, should be extended, taking culture into account as a crucial factor in the explanation of the evolution of human (literary) behavior. Gene-culture coevolution provides a sound Darwinian framework for this extended approach. Literary Darwinists sometimes refer to research in gene-culture coevolution but they mostly do not fully appreciate the extent to which — when it is used as the primary explanatory framework —, it allows developing a more sophisticated understanding of the evolution of (literary) behaviors.

Acknowledgements

I thank the Research Foundation–Flanders (FWO) for the support.

References

Andrews, P., Gangestad, S. & Matthews, D. (2002). Adaptationism – how to carry out an exap- *tationist program. Behavioral and Brain Sciences, 25, 489–553.*

Boyd, B. (2009). *On the origin of stories. Evolution, cognition and fiction. Cambridge, MA:* Harvard University Press.

Boyd, R. & Richerson, P. (1985). Culture and the evolutionary process. London & Chicago: University of Chicago Press.

Cosmides, L. & Tooby, J. (1989). Evolutionary psychology and the generation of culture, Part II. Case study: A computational theory of social exchange. Ethology and Sociobiology, 10, 51–97.

Dawkins, R. (1976). The selfish gene. Oxford & New York: Oxford University Press.

Dutton, D. (2009). The art instinct. Beauty, pleasure and human motivation. New York:

Bloomsbury Press. Ekman, P. (1992). An argument for basic emotions. Cognition and Emotion, 6, 169–200.

Rozin, P., Haidt, J., & McCauley, C. (2008). "Disgust." In M. Lewis & J. M. Haviland-Jones (Eds.), Handbook of emotions, 3rd Edition (pp. 757–776). New York: Guilford Press.

Gould, S. J. & Vrba, E. S. (1982). Exaptation: A missing term in the science of form. Paleobiology, 8, 4–15.

Gould, S. J. (1991). Exaptation: A Crucial Tool for an Evolutionary Psychology. JSI, 47, 43–65.

Heath, C., Bell, C., & Sternberg, E. (2001). Emotional selection in memes: the case of urban legends. Journal of Personality and Social Psychology, 81, 1028–41.

Kelly, D. (in press). Moral disgust and the tribal instincts hypothesis. In R. Joyce, K. Sterelny, & *B. Calcott (Eds.), Signaling, commitment and emotion. MIT Press.*

Lumsden, C. J., & Wilson, E. O. (1981). *Genes, mind and culture: The coevolutionary process.* Cambridge, MA: Harvard University Press.

Rakoczy, H., Tomasello, M., & Striano, T. (2005). On tools and toys: how children learn to act *on and pretend with ''virgin objects''. Developmental Science, 8, 57–73.*

Richerson, P., & Boyd, R. (2005). *Not by genes alone. How culture transformed human evolution.* London & Chicago: University of Chicago Press.

Sperber, D., & Hirschfeld, L. A. (2004). The cognitive foundations of cultural stability and diversity. Trends in Cognitive Science, 8, 40–46.

Striano, T., Tomasello, M., & Rochat, P. (2001). Social and object support for early symbolic play. Developmental Science, 4, 442–455.

Williams, G. (1966). Adaptation and natural selection. Princeton: Princeton University Press.

Wilson, E. O. (1999). Consilience. The unity of knowledge. New York: Vintage.

Chapter 3: The Evolutionary Significance Of The Arts – Exploring The By-Product Hypothesis In The Context Of Ritual, Precursors, And Cultural Evolution

The arts have recently become fundamental to debates on human cognitive evolution on a number of counts, with many arguing that they set humans apart from other species and are one of the main traits that define modern humans (e.g., Henshilwood and Marean 2003). As a result, evidence of early artistic behavior has given rise to intense debate. Interestingly, various artifacts have been found that increasingly consign the origins of modern human behavior to a period ever closer to when *Homo sapiens sapiens* first appeared as an anatomically modern species (*180,000 BP). Partially in response to these recent finds, the debate as to whether the arts are biologically adaptive or are more culturally derived has intensified. As the arts are central to this debate, it is essential to determine their proper place in evolution. The aim of this article is to assess the role of the arts in relation to the trajectory of human evolution in order to avoid the confusion and pitfalls that have hindered this debate.

The first part of this article will examine the relevance of aesthetics to the debate, after which we will identify the appropriate context for assessing the role of the arts and, by implication, their natural point of reference. Some recent theories that attempt to explain the arts from the perspective of evolution will then be considered in light of the foregoing. By way of illustration, specific examples from the archaeological record of how the arts were utilized by ancient peoples will be presented. Having identified the practical and theoretical standpoints for assessing the role of the arts, the ramifications arising will then be explored in the second part (''Originating Mechanisms'') with a special focus on the relationship between biological adaptation, exaptation, and by-product approaches that will be assessed within a gene-culture coevolutionary (aka dual inheritance) framework. The final section will address the consequences arising from the possibility that the arts may not be biologically adaptive. More specifically, we will claim that the evolution of the arts (not their origins) has been tightly linked to ritual and associated activities throughout the major part of evolutionary history, to the extent that they should be regarded as a complex whole. This behavioral complex, we will argue, has fitness costs for its participants that, on average, may overrule any of the evolutionary benefits deriving from each of the arts.

Setting the Context

Aesthetics and Art

Before considering these issues, the relevance of aesthetics needs to be clarified, especially as the concept is often conflated with ''art'' with regard to evolutionary explanations. Brown and Dissanayake (2009) point out that, although aesthetics may sometimes play a role in the arts, they are neither critical nor essential—a conclusion that may be correct yet is somewhat excessive, as we shall see. This reflects earlier debates on the subject in which the suggestion that aesthetics should be considered crucial to the arts was rejected by anthropologists (Weiner 1994). The main reason for this dismissal is that an overt concern for aesthetics as such only became prominent quite recently (principally in post-Renaissance European art, and especially during the 18th century with the idea of refined taste), which is in contrast to pre-literate tribal/tradition-based communities (including both ancient and modern hunter–gatherer groups, hereafter referred to as AMHGs), where such a preoccupation is accorded low priority—but which is not the same as saying they had no interest in aesthetics. To emphasize, AMHGs will have had an interest in ''beauty,'' and therefore aesthetics, but this was an aesthetic intimately linked to artifacts, which involved a concern for balance, order, symmetry, and so on, and not one of detached contemplation. Aesthetics were therefore of secondary importance to AMHGs (Dissanayake 2011), not least because the arts were employed to meet the requirements of a range of activities relating to supernatural/magical thinking (Eibl and Mellmann 2008; Carneiro 2010) and other more immediate concerns. Thus, the arts were utilized in a different way by such groups compared to how they are often referred to in the modern sense.[4] So, although a modern individual might see and emphasize the aesthetic value of artifacts from prehistory or those created by AMHGs, ''aesthetics" (even in Davies's (2012) broad sense of seeking and valuing beauty) was probably not the main concern for the authors of the original artifact(s).

For AMHGs, aesthetic concerns were therefore mainly subsidiary to the utilitarian purpose of the arts, which is borne out by Paleolithic art, where many of the depictions are ''substandard" and frequently

[4] This is exemplified in the fact that, since the beginning of the 20th century, aesthetic appeal also began to lose its central position in Western art as illustrated by the (in)famous example of Duchamp's urinal of 1917, and by the 1960s the idea of beauty had virtually disappeared from contemporary art (Danto 2003).

displayed in a haphazard, uncoordinated way. In fact, many of the depicted animals are often lost in multiple superimpositions resulting in a confused mass of lines, or were defaced, hidden, incomplete, distorted, poorly executed, or deliberately obliterated, with many sculptures intentionally smashed or buried (Bahn and Vertut 1997). The same widespread tendency to obliterate or destroy previously made ''aesthetic" artifacts can be found at the pre-Neolithic site of Göbekli Tepe dating to around 12,000 years ago (Schmidt 2010) and Çatalhöyük, around 9,000 years old (Hodder 2010). Western commentators tend to accentuate the best examples of Upper Paleolithic art because this appeals to their aesthetic inclinations and therefore foreground the flagship cave art of Lascaux, Chauvet, or Altamira, whereas the majority of the art from most of the sites (including the flagship caves) looks unfinished or is fragmented (see below for a discussion of examples from the Mesolithic and Neolithic). Thus, even though some of the depictions of AMHGs may be regarded as aesthetically pleasing to a modern sensibility, for traditionally based tribal groups this was not the overriding concern. In what follows, the emphasis will, therefore, be on investigating the art of AMHGs, in which aesthetics remain subservient to the perceived utility of the artifacts. By examining the arts from this perspective, we will be better placed to understand their true provenance.

Placing the Arts in Context

The majority of world art of the past was integral to the daily life of various communities on a number of different levels. This also applies to AMHGs, where the arts are connected to the effectiveness of the objects employed in rituals related to supernatural thinking, which explains why there is often no word for art in such cultures (Morphy 1994; Soffer and Conkey 1997; Dissanayake 1999). Moreover, even in cases where an object may seem to serve a purely practical purpose, it has been established that such objects are, in fact, associated with more animistic concerns (Ingold 2006; Hodder 2010; Vanpool and Newsome 2012). Thus, what might appear to be purely functional pottery without any decoration turns out to have additional significance that was not obvious in the first instance (Vanpool and Newsome 2012). Other similar examples include the way everyday objects, including actual houses, were intimately associated with ritual at the Neolithic site of Çatalhöyük (date * 9,000 BP) (Hodder 2010). In fact, Çatalhöyük itself is not only replete with ritualistic significance but is also thought to have originated from the need to perform rituals. As Hodder writes (2010, p.18), ''Many now argue that the reason people started agglomerating and creating settled life may have been religious ritual.'' Indeed, it is now becoming increasingly clear that fundamental changes to social and economic ways of life were due to ritual, as suggested by the pre- Neolithic site of Göbekli Tepe (date * 11,000 BP) (Schmidt 2010), and not climatic events or changes to the social fabric. Göbekli Tepe is particularly important as the people responsible for its construction were hunter–gatherers (i.e., not settled farmers), yet spent enormous amounts of time and energy constructing multiple ‘‘temples’’ where ritual practices occurred. These huge constructions were also destroyed in successive bouts— reflected in the way Upper Paleolithic paintings were regularly defaced or obliterated—suggesting the intervention of ritual tendencies. Similarly, repeated destruction of artifacts, including carefully prepared paintings, also took place at Çatalhöyük. Moreover, most anthropological/ethnographic research shows that the large bulk of artistic behavior in contemporary hunter–gatherer societies is embedded in ritual, and therefore it is reasonable to assume this was the case for the ancient hunter–gatherer societies as well when the arts first emerged. In fact, cognitive archaeologists now argue that the ability to engage in ritual is extremely ancient, perhaps stretching back 500,000 years with the onset of mythic culture (Donald 1991). Therefore, from the beginning, it seems that the arts and ritual were intimately related and did not exist as separate domains. These examples are fundamental to the present debate, as they provide concrete evidence that the earliest art may have been used mainly for ritual purposes.

Thus, the lifeways of AMHGS were invariably suffused with magical thinking to a greater or lesser extent, in that even everyday objects, which might not seem so disposed to a modern commentator, are thereby regarded. This point is crucial because it is often assumed that for AMHGs some forms of art were independent of ritual activities and animistic beliefs. On this basis, it is reasonable to propose that the arts, and by implication aesthetics, are more closely related to ritual than is assumed. This does not suppose that all art is related to ritual, as some aspects may have been purely decorative or aesthetic, yet the latter may, nevertheless, have been exploited purely to draw attention to an object’s utility in ritual. We therefore need to remain alert to the fact there is a good chance the arts were often closely related to ritual and animistic concerns both specifically and more generally.

The fact ritual was a major concern in this context has led to the proposition that the term ‘‘art’’ should be dropped and replaced by a more inclusive term, such as ‘‘artification’’ or ‘‘making special” (Dissanayake 1988; Brown and Dissanayake 2009), so that the non-functional (with no direct practical utility) is emphasized.[5] The issue of functionality is important to this discussion as it is employed and understood in

[5] Yet this, in turn, begs the question of what AMHGs themselves meant by functional, as this will have differed from the way it is defined in the modern sense, since in the latter case this depends on a reliable utilitarian outcome predicated on sound empirical evidence. In fact, for AMHGs, the world was considered suffused by and dependent on various forces and invisible agents that a person or community regarded as decisive for survival (Ingold 2006;

different ways by anthropologists and evolutionary biologists and has therefore caused some confusion in the literature. Anthropologists regard most behavior, including ritual and religion, and associated material culture, as functional in some general way (irrespective of whether this is actually the case) in that such behavior is part of the integrated social fabric of a community that serves to sustain a group (Dissanayake 2008; Moore 2012). Evolutionary biologists, however, employ the term in a much narrower sense, with specific and rigorous conditions that must be fulfilled before the requirements of functionality can be met. Confusion has arisen when scholars attempt to inadvertently impose the latter definition of functionality onto the former situation, usually by regarding the anthropological definition of functionality as synonymous with the biological one. For example, Dissanayake (2008) in a somewhat roundabout way attempts to show how ritual and the making of various artifacts are functional to a community and have a positive effect in that these activities increase social bonding. However, this does not take account of the fact these activities often have (additional) unintended negative consequences that can lead to the demise of a community, as in, e.g., the case of Easter Island where huge resources were expended to assuage the gods, necessitating the destruction of the remaining forests on which the community's ultimate survival depended (Flenley and Bahn 2003). It will be demonstrated, however, that in order to determine whether the arts are adaptive and to avoid such confusion, we need to adhere to the *rigorous* definition of functionality from evolutionary biology. In this case, the question is whether the arts—in serving ritual—gave rise to net fitness costs versus net benefits when *all* of the possible effects on the individuals concerned are considered.

By taking account of the fact that the arts are embedded in the lifeways of AMHGs as expressed in rituals through magical thinking/animism, a basis for a more pragmatic approach to understanding the arts of previous times can potentially be established. Perhaps, therefore, the reason AMHGs did not always possess a word for art is because the main preoccupation centered on ritual, whereby the objects

---

Fausto 2007; Carneiro 2010; VanPool and Newsome 2012). Thus, AMHGs did not subscribe to the modern dichotomy of functional/nonfunctional in that the significance of most, if not all things, centered on animistic agents that could potentially inhabit, in one form or another, all aspects of the world. Thus, an object from a culture might to modern humans appear purely utilitarian, but, to those originally responsible for the artifact, significance would have been accorded based on other-worldly agents (see, e.g., VanPool and Newsome 2012). This shows that Dissanayake's dichotomy between the functional and non-functional is inappropriate. From this perspective, what is regarded as practical on a functional level today is different from how this is understood by traditional hunter–gatherer groups. For example, AMHGs might hold that the weather could be influenced by appealing to invisible agents and, in this sense, is "functional" in that a particular ritual or the use of an item employed in ritual could generate the required outcome. This is different from how functionality is referred to in modern parlance where a particular utilitarian outcome results from a specified practical procedure based on a naturalistic/materialistic outlook (Carneiro 2010).

employed (today regarded as art) were produced mainly for their apparent efficacy in such practices. In addition, there would have been no separation between, on the one hand, the various objects utilized and, on the other hand, the activities invoked in ritual. From this perspective, a dynamic interaction existed between dance, visual depictions, music, chanting, and the way the world was perceived that was manifested in a range of different ritual practices.

Critics might argue that different forms of art followed different evolutionary trajectories, with some perhaps being by-products whereas others were adaptive. Yet, this separation of art forms, both from each other and from ritual practices, is a relatively recent phenomenon related to increasing specialization that took place alongside the same tendency in other areas of human activity, such as in technology during the historical period. This separation was reinforced by the dualism of Descartes where mind and matter came to be regarded as separate entities. Many archaeologists and anthropologists, however, now reject this dichotomy in that, for AMHGs, mind, body, matter, objects, and artifacts are viewed as entangled in complex ways (Hodder 2012; Malafouris 2013).

Reframing the ''Arts'' From the foregoing, the arts as practiced by AMHGs can be defined as an activity arising from the interactions between cultural evolution, which involves the capacity to learn from others, and biological evolution, that together depend on a cognitive stance that accords significance to an object within a ritualistic or animistic context whether this is expressed explicitly in an artificially contrived artifact/ activity, or is implied in a mundane item. This definition takes into account the fact that for AMHGs different activities and objects (music, dance, visual art, etc.) were employed together in a variety of ways according to the specific requirements of ritual or within the wider framework of animism that was embedded in the social milieu of a community and, as such, directed sensibilities. According to this definition, the arts gave expression to the social matrix that existed at any one time and, as they remain embedded or entangled within this milieu, can become manifest in a variety of ways (Keane 2010, who takes a similar view). This definition also takes into account that the arts did not arise simply from genetic determinants but, fundamentally, also depended on cultural transmission (Verpooten and Nelissen 2010; Chapter 7).

Recent Theories of Evolution and Art

A number of scholars have attempted to explain the arts from an evolutionary perspective with various degrees of success. For example, the evolutionary psychologists Tooby and Cosmides (2001) defend the arts as a biological adaptation by focusing on human evolved psychology. Though previously agreeing that the arts may be a byproduct of sensory processes, they later suggested the arts may, nevertheless, have evolved as an adaptation for promoting detachment from the real world thanks to a formidable imaginative capacity underwritten by a dedicated neural system, which, through decoupled cognition, helps prepare the individual for real situations. A further advantage of such an imaginative capability is that knowledge can be shared among group members, thereby raising the number of options available for future action. Put another way, human imaginative abilities enabled the individual to escape from the tyranny of the present in a way that led to a release from proximity (Gamble 1998). This then provided a means to plan for the future through mental time travel that allowed one to reflect on past and present experiences. Even though these imaginative abilities may have conferred benefits, they may also have come with costs (i.e., giving rise to additional maladaptive traits that piggyback on such benefits). Tooby and Cosmides' adaptive explanation of the arts has been criticized for being more concerned with the ability to imagine counterfactual worlds rather than specifically being about the arts (De Smedt and De Cruz 2012). However, as Leslie (1987) has stated, although the mechanism allowing imagination to occur will have been directly adaptive, the contents of imagination are culturally derived. Tooby and Cosmides, therefore, conflate the two criteria by ignoring the fact that the arts are a function of the contents of the imagination and not the mechanism itself. Thus, it is the underlying cognitive mechanism facilitating imaginative capacities, which depends on theory of mind—as well as an enhanced memory necessary for engaging in suspension of disbelief and greater social interaction—that provided the *preconditions* for the arts to exist (Hodgson 2013). In sum, imaginative capacities (as well as the capacity to imitate that enables cultural transmission of relevant innovations) can become maladaptive precisely because such capacities are prone to error, which can have deleterious consequences both for the individual and the community when acted on. Thus, if the arts derive from cultural determinants and the cognitive mechanisms (i.e., theory of mind, enhanced memory, ability to imitate, capacity to deal with deception, and so forth) have remained relatively stable, the main evolutionary cause that gave rise to the arts must be cultural evolution.[6]

[6] Not all uses of adaptive psychological mechanisms are adaptive. Thus, (1) the use of these mechanisms for art is only adaptive if, and only if, they have been selectively modified for the evolutionary function art may have. (2) They can be exaptive in cases where they increase reproductive success but without selective modification (i.e., exaptation; see below), and (3) if no benefits, they are a by-product.

Boyd and Richerson (1985, 2005; Richerson and Boyd 2001) propose, by way of dual inheritance theory, that aesthetics and the arts are the outcome of a cultural runaway process. Thus, aesthetic qualities (by which they mean the arts) are sustained as non-functional by-products of biased cultural transmission that ultimately came to be expressed as symbols. Note, however, that they postulate in later work (Boyd and Richerson 2005) that subsequently aesthetic traits and the arts are exapted to function as social markers of ethnic groups, which is not dissimilar to Dissanayake's (2008) position. Although culture evolved to promote survival by providing a means of reliably tracking and counteracting environmental change through transmitting accumulated knowledge across generations, the arts in their runaway model qualify as a culturally evolved byproduct of such cultural determinants for reasons unconnected to survival or fitness. Moreover, cultural adaptation to the environment may be constrained and the processes of cultural evolution may not always result in a fit between individuals and their environment (Sterelny 2006).

Similarly with Brian Boyd's (2009) proposition that fiction, and by implication the arts in general, are adaptive in being derived from adaptive animal play behavior. Although Boyd offers a very comprehensive account of the evolution of the arts, this thesis has been criticized not only because by-product explanations are misrepresented, but also because he fails to take into account how the arts can be alternatively explained as co-opted by-products of adaptive traits as realized in culture. Mellmann (2010) sets out these criticisms succinctly as follows:

> An alternative explanation would be that art is an eminently *cultural* behavior… . We also have to take into account the (not specifically adaptive, or even detrimental) side-effects of these adaptations and, more importantly, the *complex cultural combinations* of a multitude of instinctive tendencies and their side-effects. Those combinations were not shaped by natural selection (although they do use a number of biological substrates that were) but rather emerge every now and then in this or that culturally more or less stabilized, conventionalized form. However, in order to eliminate those behaviors from the human genetic program, natural selection would have to eliminate the biological substrates and thus also dispense with the adaptive advantages for which these substrates have been selected, and which have obviously been significant enough to outweigh the concomitant (but less stable) negative side-effects from the outset. [italics in original]

Recently, Stephen Davies (2012) has criticized approaches that have attempted to account for the arts as genetically adaptive, deriving from sexual selection or as a spandrel (by-product), as simplistic. It is to

Davies' credit that he brings attention to the inherent complexity of the arts, both as an activity and the way they interrelate with human cognitive, social, and cultural criteria, and therefore do not lend themselves to a reductive analysis based on any one of these approaches. Davies, however, proposes that despite this complexity, culture—of which the arts are a part—is intrinsic to human nature, and can therefore give rise to positive adaptive outcomes. Thus, we need to regard the arts as similarly disposed. However, as Killin (2013) points out, even though this idea is couched within a coevolutionary framework, the model is weak because not enough support is offered regarding the suggested coevolutionary agenda. Furthermore, Davies tends to play down the importance of the rudimentary precursors that gave rise to later, more complex arts. As we will endeavor to show, although culture consists of many activities extraneous to the arts that often lead to positive biological outcomes, it comes with many maladaptive/neutral effects of which the arts and ritual are primary examples.

Are the Arts Adaptive?

The preceding considerations suggest that for AMHGs, the arts served as a means of enacting various rituals or were integrated into and facilitated an animistic belief system. Moreover, even though the arts may have had very different origins, we have considered indications that this integration happened close to the original onset. From this perspective, the arts have always been intimately intertwined with both rituals and associated belief systems, and this shared association with ritual bonded them together through entanglement (Hodder 2012), forming a complex integrated behavioral whole that was only broken gradually in historic times; a process that culminated recently with the inception of modern art movements of the West where past traditions were rejected in favor of experimentation and innovation (Gombrich 1958). If correct, our approach may simplify the adaptive analysis of the arts significantly, as it conveniently allows the question to be addressed as to whether the arts *together*—instead of singly—qualify as biological adaptations, cultural exaptations, or co-opted, non-beneficial by-products of sensory biases. In addition, our thesis that the arts have been subservient to ritual and associated activities in AMHGs suggests that whether the arts were adaptive or not may depend to a significant extent on whether these activities themselves were adaptive (see below). The null hypothesis should be that the arts are not an adaptation unless robust evidence is available that proves the opposite (Williams 1966; Buss 2004). With respect to the specific case of adaptation, in his seminal account on natural selection Williams (1966) noted that it carries an onerous burden of proof. Moreover, Williams (1966, p. 11) stressed that adaptation ''should be used only as a last resort. It should not be used when less onerous principles … are sufficient for a complete explanation.'' Before addressing the question of whether the arts are adaptive, it is first necessary to consider the role of cultural inheritance in human evolution, after which alternative evolutionary explanations can be considered—principally exaptation and by-product approaches.

Unlike most other animals, humans are heavily reliant on sociocultural learning (Henrich and McElreath 2003). Culturally transmitted information has therefore a significant impact on the human behavioral phenotype and on the dynamics of human evolution. Hence, whenever an attempt is made to reconstruct the evolutionary genesis of a particular aspect of complex human behavior and ask whether this is an adaptation or not, it is necessary, in addition to genetic evolution, to investigate the possible role of cultural evolution in its establishment as a persistent component of human nature. This requires some additional explanation. Standard evolutionary theory (i.e., the Modern Synthesis) as utilized in sociobiology and classic evolutionary psychology assumes that changes upon which natural selection can act predominantly arise from gene mutations. However, in accounts that take cultural evolution seriously, as in the gene-culture coevolutionary account, changes in the human behavioral phenotype may originate culturally from population dynamics as a result of adaptive social learning biases (Boyd and Richerson 1985; Richerson and Boyd 2005). These culturally inherited changes may subsequently result in selection for specific gene mutations that further enhance the benefits of a culturally evolved behavior, i.e., ''culture-led gene-culture coevolution'' (Richerson et al. 2010). However, these subsequent genetic modifications do not always occur. For example, it is unlikely that the evolution of the ability to read or drive a vehicle coincided with selective retention of specific gene mutations to support these abilities. Yet, such abilities may be potentially beneficial from an evolutionary perspective.

An adaptation is a trait that has been selectively modified genetically and is currently maintained for an evolutionary beneficial effect for a particular trait (i.e., increasing reproductive success). An exaptation also has an evolutionary beneficial effect but, in contrast, has not been selectively altered genetically for a particular trait (Andrews et al. 2002). This is consistent with Gould's view on exaptation (Gould and Vrba 1982; Andrews et al. 2002 discuss this in detail). Gould clearly points out that although feathers for insulation were exapted at some point in the history of flight, any subsequent genetically inherited phenotypic modifications feathers underwent for flight are ''secondary adaptations," not exaptations. Some human traits, however, may originate, evolve, and persist without any correlated genetic changes; again, it seems unlikely that literacy or the ability to drive a vehicle has been genetically selected, nevertheless both may provide significant benefits (even in evolutionary terms). Such traits can be best described as ''cultural exaptations'' because they are beneficial and culturally evolved without genetic modifications. Thus, literacy is a cultural exaptation of preexisting abilities (such as dexterity, sight, and language). Also note that literacy and the ability to become literate are nearly universal in contemporary humans (world literacy is currently nearing 90 % according to UNESCO). Thus, universality of a trait is not always a dependable indication of adaptation.

Finally, a by-product is a trait that did not evolve because it was selectively advantageous, but because it was a by-product of selection for another trait. To give another example, some culturally acquired traits may be maintained merely because they are pleasurable, or in Pinker's (1997) terms, because they ''push our pleasure buttons,'' such as is the case with drugs, pornography, and the arts (but not literature). Indeed, such nonfunctional but pleasurable traits may persist as long as they are not countered by natural selection.

Although it is often difficult to identify in practice, theoretically adaptation and the above-cited alternatives can be regarded as mutually exclusive. Whether the arts qualify as an adaptation, exaptation, or by-product depends on answers to the two following questions. First, are the arts evolutionarily beneficial (i.e., do they increase reproductive success of those that engage in the arts)? If not, a by-product explanation is likely to be the case. If the answer is yes, the arts can either be an adaptation or exaptation. To distinguish between these two options, a second question needs to be answered: have the underlying motivation and capacities for art behavior been selectively altered genetically for a beneficial effect? If the answer is affirmative, the arts qualify as an adaptation. If not, the arts qualify as an exaptation. Finally, if it can be demonstrated that the arts are the result of cultural rather than genetic changes, the arts can be viewed as ''culturally evolved" rather than genetically evolved. Thus, in conclusion, and depending on the answers to the above questions, the arts may be a genuine adaptation, a (culturally evolved) exaptation, or a (culturally evolved) by-product.

Thus, even though the arts may be intimately related to culture, as will be shown in the section on sensory biases, the activity can lead to negative or neutral effects as a result of which it may incur net fitness costs but nevertheless continue to be evolutionary maintained. The question then arises as to why the arts depend on cultural transmission.

For culture to occur, social transmission of ''information'' (i.e., ideas, beliefs, skills, knowledge, behavior) is required, but this also entails individuals remain gullible to the beliefs and influence of others (Boyd and Richerson 1985). As the arts are one of the main ways by which transmission of ideas and beliefs takes place via ritual, they are prone to a range of maladaptive tendencies. Indeed, the central claim of our exploration of the by-product hypothesis of art is that ritual can be said to constitute one of the main vehicles by which maladaptive behavior is transmitted.

Originating Mechanisms: The Arts and Sensory Biases

Although various scholars have proposed that the arts are an adaptation (see, e.g., Wilson 1998; Miller 1999, 2001; Boyd 2005; Carroll 2008; Dissanayake 2008, 2010; Dutton 2009), one of the major criticisms of this hypothesis is the fact that no dedicated areas of the brain have been found that engage art (De Smedt and De Cruz 2012). Rather many areas are recruited that invariably involve sensory and emotional/social neural networks that evolved to deal with problems of survival unrelated to the arts (Aiken 1999; Hodgson 2003; Dehaene and Cohen 2007; Zaidel et al. 2013), e.g., the discrimination of color and pattern for locating food and predators, emotion for regulating fight or flight and interactions between individuals, social factors associated with cooperative and altruistic behavior including the detection of deception, and so on. Given this, it seems unlikely that any part of the brain will have evolved specifically for the purpose of engaging in different arts. This is supported by the fact that the arts perform many different functions depending on cultural context, in the sense that, as an expressive vehicle of ritual, they can have radically different connotations and uses.

Although some universal factors are associated with the arts, which have been cited as evidence for functional adaptation/exaptation (Dissanayake 1995; Boyd 2009; Dutton 2009), these can be explained by the intrinsic appeal of the initiating sensory systems that evoke a nonbeneficial response. Thus, a particular art form is ‘‘carried along’’ with traits that have an adaptive functional design due to the fact that it is coupled with such adaptations, similar to how heat is a by-product of a light bulb (Buss 2004). Moreover, as the arts encompass a vast range of activities, behaviors, and abilities that vary greatly between groups, we need to specify exactly which are universal, a project that seems untenable.

From the outset, it should be emphasized that referring to the arts by such terms as ‘‘sensory cheesecake” (Pinker 1997) somewhat trivializes their importance, as this implies the behavior simply diverged from, or existed alongside, more pressing evolutionary concerns. As the arts have been central to the lifeways of most communities throughout time, which has been repeatedly documented by various authorities (Dissanayake 1988, 1995), the preoccupation is crucial to understanding human behavior. The thesis that art is a by-product is however not inconsistent with the observation that it is intricately intertwined with evolved traits that are functional. Therefore, perhaps the phrase ‘‘an inevitable consequence of the interactions between brain function and cultural transmission'' would provide a less pithy but more accurate description that reflects the ''necessary by-products'' of Gould and Lewontin (1997). The question then arises as to the relationship that exists between brain function, adaptation, culture, and the arts. In order to address this issue, we need first to identify the evolutionary precursors in the predisposing sensory systems.

Preexisting biases of the female perceptual system (whether incidental by-products of how neural networks are structured or functionally maintained because they are/ were adaptive in another context) can become co-opted in the mating system of a species (Ryan 1990, 1998; Arak and Enquist 1993, 1995). For example, the bowers constructed by male bowerbirds to attract females are thought to have first derived from exploitation of a sensory bias in females that was originally directed towards foraging for food such as fruit. This became useful to females in mate selection in that the bowers reduced the search parameters previously required for identifying preferred males (Madden and Tanner 2003). Sometimes, however, exploitation of sensory biases of receivers may not subsequently adaptive for receivers, in which case the evolutionary process corresponds to the strict version of sensory exploitation (Ryan 1998).

Verpooten and Nelissen (2010) (Chapter 7) highlight one such mechanism in fiddler crabs where, although females are attracted to the sand burrow entrance hoods made by courting male crabs, males are also attracted to the same hoods as a result of ''sensory trap.'' This process occurs through self-exploitation of the presenting stimulus. Similarly, the female guppy's preference for the orange spots of male guppies stems from a preference for orange food that is maintained by the fact that it is useful for obtaining such nourishment (Arnqvist 2006). These preferences, however, are accidental consequences that derive from, but remain decoupled from, the originating adaptive mechanism.

Thus, sensory exploitation based on sensory biases is widespread in the natural world, and, although it is thought to have led to and is associated with sexual selection, at the same time it is also found in many other kinds of behavior unconnected with mate preference (Arnqvist 2006). Sensory bias therefore predicts that preferences for and sensitivities to particular kinds of stimuli can exist before coevolution between aesthetic preferences and aesthetic traits has had an influence by provoking interest, thus establishing sensory bias as a critical mechanism in itself. Sensory biases may also become exploited through culturally transmitted signals. For example, humans have a strong bias for faces, due to an extremely sensitive face detection system (Johnson 2011). This bias is likely maintained by natural selection since humans rely heavily on social interactions in which face detection and recognition play a crucial role. However, the original function is obviously not maintained in the context of perceiving an artifact depicting a face, such as a mask (Sperber and Hirschfeld 2004)—a ‘‘fake’’ stimulus that became an abundant part of human material culture. Sensory exploitation by such culturally evolved signals has been shown to be relevant to understanding the evolution and persistence of cultural content attuned to our sensory systems (Verpooten and Nelissen 2010; Chapter 7).

Evidence from Nonhuman Primates

The notion that the arts are a non-adaptive/non-functional by-product of sensory systems is supported by studies of chimpanzees. The relevance of considering art-like behavior in nonhuman primates derives from the fact that, if it can be demonstrated that such behavior exists, this would provide evidence that the arts in humans are indeed a by-product of sensory mechanisms. This is because artlike activity is not part of the natural behavioral repertoire of nonhuman primates. Therefore, if nonhuman primates are able to spontaneously produce and take an interest in art-like behavior, this could only arise as a consequence of already adapted neural mechanisms that exist for reasons unconnected with the arts. This methodology is also used in sensory bias research, where the existence of a pre-existing bias is assessed by testing whether it is latently present in closely related species in which it is not naturally exploited (Ryan 1998).

Research in captive chimpanzees indicates they have an intrinsic motivation to draw in that the visible traces produced are self-reinforcing (Morris 1962; Tanaka et al. 2003), which is thought to be related to exploratory (search) behavior. Even at eleven months of age, chimpanzees take a spontaneous interest in drawing basic lines on an electronic finger touch screen (Tanaka et al. 2003). The fact that infant chimpanzees freely indulge in drawing suggests this is not adaptive but that pleasure is taken in stimulating existing psychosensory systems related to exploratory behavior, of which only the latter is adaptive. As chimps have not been observed making similar marks in the wild, this, again, suggests mark making exploits preexisting psychosensory systems. The fact that the intrinsic motivation to draw is not expressed in chimpanzees in their natural habitat is obviously because they do not possess a material culture that lends itself to creative drawing. The crucial difference, therefore, between human and nonhuman primates with respect to art making may not just be psychological but also sociocultural. Interestingly, chimpanzees possess enough manual dexterity to both produce and complete iconic images but are unable to succeed in this due to a lack of visual memory capacity (Saito et al. 2010).

Similarly, music exploits the neural mechanisms of auditory processing (Changizi 2011), which is supported by the fact that monkeys, who are unable to produce music, respond in a consistent way to species-specific natural calls synthesized and played back as ''music.'' Moreover, they are also able to recognize tonal diatonic melodies, as opposed to the chromatic scale or atonal sounds, though this does not generalize to melodies transposed to different keys (Hauser and McDermott 2003; Snowdon and Teie 2010). As Snowdon and Teie (2010, p. 30) state, ''Tamarins were generally indifferent to playbacks of human music, but responded with increased arousal to tamarin threat vocalization based music, and with decreased activity and increased calm behavior to tamarin affective vocalization based music.''

In addition, research of (admittedly one) chimpanzee indicates a sensitivity to, and tendency for synchronous movement (tapping) in response to an auditory rhythm (Hattori et al. 2012); a finding, if corroborated, that reflects the above studies of mark making in chimpanzees. Music, therefore, seems to engage phylogenetically ancient auditory mechanisms related to the soundscape important to species' survival but which did not evolve for the purpose of music appreciation (Changizi 2011; De Smedt and De Cruz 2012). Thus, certain rudimentary sensory mechanisms that were biologically adaptive may have been recruited for added purposes. Evolution always needs to build on what already exists, so nonhuman precursors will be found to a certain extent. However, these homologous precursors may or may not be recruited for novel purposes in the subsequent independent evolution of different species. As outlined, some monkeys, although not responding to music derived from human speech, do so to music based upon their own species-specific vocalizations (Snowdon and Teie 2010). Within our species this principle is indicated by the observation that most, but not all, scales throughout time employ between five and seven tones, which may be related to the fact that the pentatonic and heptatonic natural scales correlate with the way human speech is perceived (Gill and Purves 2009). In this regard, De Smedt and De Cruz (2010) note that the reconstruction of the 36,000- year-old bone flute from Geißenklösterle in Germany produces tones that fall within the minor pentatonic scale (Seeberger 2003)—a scale that is most widely exploited cross-culturally. Musical appreciation may therefore have either originally derived, or alternatively developed, in tandem with previously adapted vocalizing capacities that were co-opted by culture for active musical purposes. However, despite the fact that research suggests that some very basic auditory traits for musicality appear to exist in very young human infants, the majority of what are commonly accepted as musical skills are thought to be culturally determined (Hannon and Trainor 2007).

In summary, research on nonhuman primates suggests they spontaneously engage in non-adaptive art-like activities that derive from the pleasure of engaging in sensory systems that evolved for adaptive reasons, such as search behavior or species-specific calls. Although such fundamentals may seem remote from the artistic behavior of humans, they nevertheless provided a ''template'' from which complex artistic activities could be realized. The most parsimonious[7] hypothesis, then, would be that the arts recruit primate and species-specific building blocks or precursors, without giving rise to net benefits for individuals. Thus, the by-product explanation should be favored as the null hypothesis unless strong indications are found that the arts confer fitness benefits for which they were selected (i.e., adaptation) or not (i.e., exaptation).

The Cognitive Niche of the Arts and Sensory Biases

Thus, the ''arts'' may derive from the exploitation of preexisting psycho-sensory correlates through resonance that served as the main driving force in the evolution of artistic behavior (Hodgson 2000, Hodgson and Helvenson 2006; Pinker 1997; Verpooten and Nelissen 2010; Chapter 7). In other words, the adaptive mechanism that originally gave rise to neural networks tends to resonate with stimuli similar to that which first led to the formation of a particular neural system. In this sense, the arts can be said to be co-opted (beneficial or not) from preexisting adaptive mechanisms that became important in the cultural domain. From this perspective, the arts conveniently mesh with existing human cognitive abilities and were thereby subject to cultural selection through sensory exploitation (Verpooten and Nelissen 2010; Chapter 7). Likewise, neural resonance corresponds to what is termed ''content biases,'' which are transmissible features that are intrinsically memorable or easily accessed due to their close relationship to the structure of the mind (Shennan 2008). The important point here is that even though human minds are generally adaptive and have adaptive functions, they are also prone to produce and prefer *fitness-neutral* behaviors, ideas, beliefs, and values that often become maladaptive in a given context due to latent biases and biases that are functionally maintained in another context (Henrich and McElreath 2003).

Art and Ritual: Non-beneficial Practices?

Rituals are commonly considered useful or beneficial in some way (Gino and Norton 2013), whether or not their use is cashed out in the currency of fitness and thus would count as truly evolutionary beneficial. However, arguably, many specific kinds of ritual (which are invariably replete with art), especially those

---

[7] We mean *relative* parsimony, as traded against model complexity (i.e., goodness of fit), and not parsimony in absolute terms as in the principle of Occam's razor, since parsimony is not defensible in the generalized way implied by Occam's razor (Sober 2006).

that are costly, may not be beneficial. As an irrational means of attempting to control the world, much time and effort is expended in the pursuit of ritual for little or no positive outcome—the many ways in which ritual and associated activities were self-destructive to AMHGs has been aptly catalogued by Edgerton (1992) and Carneiro (2010). In this context, ritual, rather than being regarded as adaptive in a general sense (i.e., culturally adaptive) in being functionally useful for sustaining a group (see, e.g., Rappaport 1999; Sosis 2000), is viewed as a by-product of an enduring sensory and cognitive mechanism relating to a precaution/hazard warning system—the proper adaptive domain (Boyer and Lie´nard 2008). Hence, ritual developed out of the need for social affiliation that gave what apparently appeared to be control of the environment but which was largely misplaced and therefore, in this sense, was maladaptive, which is a tendency that increased as societies became more hierarchical and prescriptive. Therefore, although ritual, and ultimately religion, may have helped strengthen group cohesion, this was offset by the fact that such behavior was also misapplied in the sense that it was utilized for the control of natural disasters or events that were perceived as capable of being influenced by appealing to other worldly agents. In this regard, rather than ritual and the arts, it was probably prosocial behavior together with increased organizational abilities and foresight that were the main adaptive driving forces in human survival. Thus, as the arts for AMHGs were mainly subservient to ritual, it follows that such activity would generally also have led to maladaptive or evolutionary neutral net outcomes—even though ritual may *occasionally appear* to have been adaptive in certain contexts. Due to the fact that ritual and associated arts were unable to track or deal with evolutionary threats to survival with any great reliance, it is therefore parsimonious to assume they were not adaptive in a critical sense.

Interestingly, the universal proclivity for supernatural thinking in AMHGs (which continues in the contemporary world) may be a necessary consequence of how the brain has gravitated towards greater neural density, proliferation, reorganization, and neural transmission speed. In this scenario, neural signals tend to increasingly overlap, especially within and between modular structures (Kaas 2008) thus giving rise to conscious awareness, social abilities, imaginative faculties, and deceptive capacities (Dehaene and Naccache 2001; Ghazanfar 2008; Konopka et al. 2012). As one is susceptible to being lured by the arts, and most of the arts are about a willingness to participate in reciprocal deception (Hodgson and Helvenson 2006; Hodgson 2013), one was also liable to indulge in communal playacting that enacted various cultural myths as typified in rituals. Although this may sometimes appear to increase group bonding, at the same time, it may have been more than cancelled out by the irrational behavior associated with ritual practices. Maladaptive behavior is a common symptom of human endeavor and is the cost paid for a large, complex brain and flexible cognition that subserves the associated sociocultural milieu, where ritual represents one example of such a cost that is carried along with adaptive behavioral correlates. As Boyd and Richerson (2007, p. 328) state, culture ''comes with a built-in tradeoff: culture provides a rich source of adaptive information, but to use it efficiently individuals have to be 'credulous,' mainly adopting the beliefs of those around them and this credulity allows maladaptive beliefs to spread.'' This explains why maladaptive traits such as rituals were not culled.

As the arts primarily served the purpose of ritual, the question then becomes, why is ritual so pervasive in human behavior? Ritual is associated with anxiety and, when chronic, becomes compulsive, which is manifest in ritualized actions as a short-term means of assuaging raised levels of anxiety that leads to even greater anxiety in the medium to long term (Fiske and Haslam 1997; Boyer and Lie´nard 2008). Ritualized actions mainly involve behavior that becomes detached from the originating cause through displacement, which provides short-term reassurance by imposing order in the face of perceived insecurity/danger. Repetitive behavior is closely associated with anxiety, and, as redundancy is also a defining feature of collective ritual, ritual may have arisen as an irrational means of assuaging perceived threat that subsequently came to be expressed culturally as a means of combating such threat (whether real or imaginary). Boyer and Liénard (2008) see this as deriving from human vigilance—a precaution/hazard warning system that monitors potential danger, thus spurring the individual towards taking aversive action. However, although anxiety is a normal adaptive function that prepares the individual for threat, it becomes maladaptive when chronic. Collective cultural rituals share many of the features of such chronic conditions, especially with regard to rigidity and inflexibility when the emphasis is placed on the procedure rather than the goal (Fiske and Haslam 1997; Boyer and Liénard 2008). Rituals are therefore compelling because the human cognitive system makes such a behavioral repertoire attention grabbing (Liénard and Boyer 2006), which thereby becomes liable to cognitive capture that has much in common with the aforementioned sensory trap. Interestingly, small groups appear to practice what are termed imagistic rituals (as opposed to the doctrinal rituals of settled communities), which are characterized by potent emotions and traumatic practices full of intense imagery (i.e., art) that often give rise to extreme behavior (Atkinson and Whitehouse 2011), and which are likely to have been the type of ritual favored by hunter–gatherers during the Upper Paleolithic and pre-Neolithic (as evidenced by the aforementioned examples). Thanks to the high attention load, rituals and associated belief systems therefore become an excellent means for transmitting cultural information (not always beneficial), which persisted as a parasitic by-product of the original adaptive mechanism, as is now being increasingly emphasized (Liénard and Boyer

2006; Boyer and Liénard 2008; Atran and Henrich 2010). It follows that if ritual is a non-beneficial by-product of primary adaptive mechanisms, given that the main outlet for art is through ritual, then most of the arts may also be a non-beneficial by-product.

Discussion

As we have stipulated, although the arts may be viewed as culturally maintained by-products of enduring evolutionary precursors, this does not therefore mean they do not have important consequences for human endeavor. Moreover, we have developed in detail a specific variant of the null hypothesis, which proposes that the arts are neither an adaptation nor an exaptation but rather sustained as a nonfunctional by-product of such factors. Gene-culture coevolution has, however, been cited as an explanation for the prevalence of the arts (De Smedt and De Cruz 2012; Killin 2013), which is not incompatible with the above analysis, as the cultural part of this interrelationship can also give rise to neutral and maladaptive tendencies. As stipulated, culture appears to have arisen as a means of swiftly adapting to novel and changing environments that required a long period of learning and a degree of flexibility, by providing a means of transmitting information from one generation to the next which, although adaptive, also came with maladaptive costs (Boyd and Richerson 1985, 2005). This also fostered a tendency for magical thinking whereby the inanimate and animate were liable to be regarded as an extension of human cognitive faculties (Helvenston and Hodgson 2010). Although some aspects of ritual-like behavior may seem to have been adaptively beneficial, these may have been more than offset by the many instances where ritual led to maladaptive outcomes, e.g., the many examples of ritualized infanticide carried out in pre-Columbian Central and South America, as well as other parts of the world, where the remains of children became ritualized art objects with many infants thought to have been voluntarily donated by biological parents to appease the gods (De La Cruz et al. 2008). In the last analysis, the ‘‘sapient paradox” of Renfrew (2008) in which complex culture, i.e., the arts, did not predominate until sometime after the speciation of *Homo sapiens sapiens*, suggests that, in conjunction with limited population levels, the behavioral trait that may have hindered this centered on a continued reliance on ritual and magical/ animistic thinking thereby preventing a more considered assessment of real practical issues.

Conclusion

The above evidence suggests that the arts did not evolve as adaptations, but rather arose as a non-beneficial by-product of certain long-standing psychosensory biases, which were duly co-opted by the arts in the context of ritual as a result of cultural evolution. As the arts evolved culturally, this allowed their qualities to be exploited in either neutral or maladaptive ways depending on circumstances. Having said this, it needs to be emphasized that when ‘‘culture’’ is referred to in this context, we are referring to a capacity for culture (i.e., evolved social learning abilities) that was itself adaptive by way of individual or group selection, and the arts are a product of this capacity. In this way, ritual behavior and the arts may have been an inevitable but costly non-functional by-product of such a capacity that was realized in culture. It may therefore be time to move away from explanations based on traditional evolutionary psychology and straightforward adaptive explanations that do not take cultural evolution as an independent force in human evolution seriously, and concentrate on more fruitful avenues of research based on a coevolutionary framework involving culture. In view of the above observations, accounts based on traditional evolutionary psychology that have sought to explain the arts have not met the robust requirements that are essential for such claims to be verified. In coming to this conclusion, it has been necessary to examine evidence from diverse fields including neuroscience, cognitive evolution, archaeology, behavioral ecology, and related disciplines, which strongly suggest that alternatives to adaptation, especially the by-product hypothesis offered here, cannot currently be refuted.

Acknowledgments

JV thanks the Research Foundation Flanders (FWO) for support (Grant no. G085012N).

References

Aiken N (1999) How art arouses emotion. In: Bedaux B, Cooke B (eds) Sociobiology and the arts. Rodopi, Amsterdam, pp 159–173

Andrews P, Gangestad S, Matthews D (2002) Adaptationism: how to carry out an exaptationist program. Behav Brain Sci 25:489–553

Arak A, Enquist M (1993) Hidden preferences and the evolution of signals. Phil Trans R Soc B 340:207–213

Arak A, Enquist M (1995) Conflict, receiver bias and the evolution of signal form. Phil Trans R Soc B 349:337–344

Arnqvist G (2006) Sensory exploitation and sexual conflict. Phil Trans R Soc B 361:375–386

Atkinson QD, Whitehouse H (2011) The cultural morphospace of ritual form: examining modes of religiosity cross-culturally. Evol Hum Behav 32:50–62

Atran S, Henrich J (2010) The evolution of religion: how cognitive by-products, adaptive learning heuristics, ritual displays, and group competition generate deep commitments to prosocial religions. Biol Theory 5:18–30

Bahn PG, Vertut J (1997) Journey through the Ice Age. Weidenfeld and Nicolson, London

Boyd B (2005) Evolutionary theories of art. In: Gottschall J, Wilson DS (eds) The literary animal. Northwestern University Press, Evanston, pp 149–178

Boyd B (2009) On the origin of stories: evolution, cognition, and fiction. Belknap Press of Harvard University Press, Cambridge Boyd R,

Richerson PJ (1985) Culture and the evolutionary process. University of Chicago Press, Chicago

Boyd R, Richerson PJ (2005) The origin and evolution of cultures. University of Chicago Press, Chicago

Boyd R, Richerson PJ (2007) Cultural adaptation and maladaptation: of kayaks and commissars. In: Gangestad S, Simpson J (eds) The evolution of mind: fundamental questions and controversies. Guilford, New York, pp 327–331

Boyer P, Liénard P (2008) Ritual behavior in obsessive and normal individuals: moderating anxiety and reorganizing the flow of action. Curr Dir Psychol Sci 17:291–294

Brown S, Dissanayake E (2009) The arts are more than aesthetics: neuroaesthetics as narrow aesthetics. In: Skov M, Vartanian O (eds) neuroaesthetics. Baywood, Amityville, pp 43–57

Buss DM (2004) Evolutionary psychology: the new science of the mind. Pearson, Boston

Carneiro RL (2010) The evolution of the human mind: from supernaturalism to naturalism—an anthropological perspective. Eliot Werner, New York

Carroll J (2008) An evolutionary paradigm for literary study. Style 42:103–425

Changizi M (2011) Harnessed: how language and music mimicked nature and transformed ape to man. Benbella Books, Dallas

Danto A (2003) The abuse of beauty: aesthetics and the concept of art. Open Court, Chicago

Davies S (2012) The artful species: aesthetics, art, and evolution. Oxford University Press, Oxford

De La Cruz I, Gonzalez-Oliver A, Brian MK et al (2008) Sex identification of children sacrificed to the ancient Aztec rain gods in Tlatelolco. Curr Anthropol 49:519–526

De Smedt J, De Cruz H (2010) Toward an integrative approach of cognitive neuroscientific and evolutionary psychological studies of art. Evol Psychol 8:695–719

De Smedt J, De Cruz H (2012) Human artistic behavior: adaptation, byproduct, or cultural group selection? In: Plaisance KS, Reydon TAC (eds) Philosophy of behavioral biology. Springer, Dordrecht, pp 167–187

Dehaene S, Cohen L (2007) Cultural recycling of cortical maps. Neuron 56:384–398

Dehaene S, Naccache L (2001) Towards a cognitive neuroscience of consciousness: basic evidence and a workspace framework. Cognition 79:1–37

Dissanayake E (1988) What is art for? University of Washington Press, Seattle

Dissanayake E (1995) Homo aestheticus: where art comes from and why. University of Washington Press, Seattle

Dissanayake E (1999) ''Making special'': an undescribed human universal and the core of a behavior of art. In: Cooke B, Turner F (eds) Biopoetics. ICUS, Lexington, pp 27–46

Dissanayake E (2008) The arts after Darwin: does art have an origin and adaptive function? In: Zijlmans K, Van Damme W (eds) World art studies: exploring concepts and approaches. Valiz, Amsterdam, pp 241–263

Dissanayake E (2010) The deep structure of Pleistocene rock art: the ''artification hypothesis.'' Pré-actes du congrès, IFRAO Ariége 2010, Pleistocene art of Europe, Lacombe, Tarascon-sur-Ariége. http://ifrao.sesta.fr/docs/Articles/Dissanayake-Signes.pdf

Dissanayake E (2011) ''My glyph is more beautiful than yours'' —but does it matter? Rock Art Res 28:168–171

Donald M (1991) Origins of the modern mind: three stages in the evolution of culture and cognition. Harvard University Press, Cambridge

Dutton D (2009) The art instinct. Oxford University Press, Oxford

Edgerton RB (1992) Sick societies: challenging the myth of primitive harmony. Free Press, New York

Eibl K, Mellmann K (2008) Misleading alternatives. Style 42:166–171

Fausto C (2007) Feasting on people: eating animals and humans in Amazonia. Curr Anthropol 48:497–530

Fiske AP, Haslam N (1997) Is obsessive-compulsive disorder a pathology of the human disposition to perform socially meaningful rituals? Evidence of similar content. J Nerv Ment Dis 185:211–222

Flenley J, Bahn P (2003) The enigmas of Easter Island. Oxford University Press, Oxford

Gamble C (1998) Paleolithic society and the release from proximity: a network approach to intimate relations. World Archaeology 29:426–449

Ghazanfar AA (2008) Language evolution: neural differences that make a difference. Nat Neurosci 11:382–384

Gill KZ, Purves D (2009) A biological rationale for musical scales. PLoS One 4:e8144

Gino F, Norton, MI (2013) Why rituals work. Scientific American. URL: http://www.scientificamerican.com/article/why-ritualswork/

Gombrich EH (1958) The story of art. Phaidon, London

Gould SJ, Lewontin RC (1997) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc R Soc London B 205:581–598

Gould SJ, Vrba ES (1982) Exaptation: a missing term in the science of form. Paleobiology 8:4–15

Hannon EE, Trainor LJ (2007) Music acquisition: effects of enculturation and formal training on development. Trends Cogn Sci 11:467–472

Hattori Y, Masaki T, Matsuzawa T (2012) Spontaneous synchronized tapping to an auditory rhythm in a chimpanzee. Sci Rep 3:1566. doi:10.1038/srep01566

Hauser MD, McDermott J (2003) The evolution of the music faculty: a comparative perspective. Nat Neurosci 6:663–668

Helvenston PA, Hodgson D (2010) The neuropsychology of ‘‘animism’’: implications for understanding rock art. Rock Art Res 27:61–94

Henrich J, McElreath R (2003) The evolution of cultural evolution. Evol Anthropol 12:123–135

Henshilwood CS, Marean CW (2003) The origin of modern human behavior. Curr Anthropol 44:627–651

Hodder I (2010) Probing religion at Çatalhöyük: an interdisciplinary experiment. In: Hodder I (ed) Religion in the emergence of civilization: Çatalhöyük as a case study. Cambridge University Press, Cambridge, pp 1–31

Hodder I (2012) Entangled: an archaeology of the relationships between humans and things. Wiley-Blackwell, Chichester

Hodgson D (2000) Art, perception and information processing: an evolutionary perspective. Rock Art Res 17: 3–34

Hodgson D (2003) The biological foundations of Upper Palaeolithic art: stimulus, percept and representational imperatives. Rock Art Res 20:3–22

Hodgson D (2013) Ambiguity, perception, and the first representations. In: Sachs-Hombach K, Schirra JRJ (eds) Origins of pictures. Papers from the Chemnitz conference, Germany 2010. Halem, Köln, pp 401–423

Hodgson D, Helvenson PA (2006) The emergence of the representation of animals in palaeoart: insights from evolution and the cognitive, limbic and visual systems of the human brain. Rock Art Res 23:3–40

Ingold T (2006) Rethinking the animate, re-animating thought. Ethnos 71:9–20

Johnson MH (2011) Face perception: a developmental perspective. In: Calder A, Rhodes G, Johnson M et al (eds) Oxford handbook of face perception. Oxford University Press, New York, pp 3–14

Kaas JH (2008) The evolution of the complex sensory and motor systems of the human brain. Brain Res Bull 75:384–390

Keane W (2010) Marked, absent, habitual: approaches to Neolithic religion at Çatalhöyük. In: Hodder I (ed) Religion in the emergence of civilization. Çatalhöyük as a case study. Cambridge University Press, Cambridge, pp 187–219

Killin A (2013) The arts and human nature: evolutionary aesthetics and the evolutionary status of art behaviours. Biol Philos 28:703–718

Konopka G, Friedrich T, Davis-Turak J et al (2012) Human-specific transcriptional networks in the brain. Neuron 75:601–617

Leslie M (1987) Pretense and representation: the origins of ''theory of mind.'' Psychol Rev 94:412–426

Liénard P, Boyer P (2006) Whence collective rituals? A cultural selection model of ritualized behavior. Am Anthropol 108:814–827

Madden JR, Tanner K (2003) Preferences for colored bower decorations can be explained in a nonsexual context. Anim Behav 65:1077–1083

Malafouris L (2013) How things shape the mind: a theory of material engagement. MIT Press, Cambridge

Mellmann K (2010) The multifunctionality of idle afternoons. Art and fiction in Boyd's vision of evolution [review of Boyd 2009]. J Lit Theory online (09.03.2010). URL: http://www.jltonline.de/index.php/reviews/article/view/170/530

Miller GF (1999) Sexual selection for cultural displays. In: Dunbar R, Knight C, Power C (eds) The evolution of culture. Edinburgh University Press, Edinburgh, pp 71–91

Miller GF (2001) Aesthetic fitness: how sexual selection shaped artistic virtuosity as a fitness indicator and aesthetic preferences as mate choice criteria. Bull Psychol Arts 2:20–25

Moore JD (2012) Visions of culture: an introduction to anthropological theories and theorists. AltiMira, Plymouth

Morphy H (1994) The anthropology of art. In: Ingold T (ed) Companion encyclopedia of anthropology. Routledge, London, pp 648–685 Morris D (1962) The biology of art. Methuen, London

Pinker S (1997) How the mind works. Norton, New York

Rappaport RA (1999) Ritual and religion in the making of humanity. Cambridge University Press, New York

Renfrew C (2008) Neuroscience, evolution and the sapient paradox: the factuality of value and of the sacred. Philos Trans R Soc London B 363:2041–2047

Richerson PJ, Boyd R (2001) Built for speed, not for comfort: darwinian theory and human culture. Hist Phil Life Sci 23:425–465

Richerson PJ, Boyd R, Henrich J (2010) Gene-culture coevolution in the age of genomics. Proc Natl Acad Sci USA 107:8985–8992

Ryan MJ (1990) Sexual selection, sensory systems and sensory exploitation. Oxford Surv Evol Biol 7:157–195

Ryan MJ (1998) Sexual selection, receiver biases, and the evolution of sex differences. Science 281:1999–2003

Saito A, Hayashi M, Takeshita H et al (2010) Drawing behavior of chimpanzees and human children: the origin of representational drawing. In: Proceedings of the third international workshop on Kansei, Fukuoka, Japan, 22–23 Feb 2010

Schmidt K (2010) Göbekli Tepe—the Stone Age sanctuaries: new results of ongoing excavations with a special focus on sculptures and high reliefs. Documenta Praehistorica 37:239–256

Seeberger F (2003) Klangwelten der Altsteinzeit. CD recorded for Urgeschichtliches Museum, Blaubeuren

Shennan S (2008) Canoes and cultural evolution. Proc Natl Acad Sci USA 105:3175–3176

Snowdon CT, Teie D (2010) Affective responses in tamarins elicited by species-specific music. Biol Lett 6:30–32

Sober E (2006) Parsimony. In: Sarkar A, Pfeifer J (eds) The philosophy of science: an encyclopedia. Routledge, New York, pp 531–538

Soffer O, Conkey MW (1997) Studying ancient visual cultures. In: Conkey M, Soffer O, Stratmann D et al (eds) Beyond art: Pleistocene image and symbol. California Academy of Sciences, San Francisco, pp 1–16

Sosis R (2000) Religion and intragroup cooperation: preliminary results of a comparative analysis of utopian communities. Cross- Cult Res 34:70–87

Sperber D, Hirschfeld LA (2004) The cognitive foundations of cultural stability and diversity. Trends Cogn Sci 8:40–46

Sterelny K (2006) The evolution and evolvability of culture. Mind Lang 21:137–165

Tanaka M, Tomonaga M, Matsuzawa T (2003) Finger drawing by infant chimpanzees (*Pan troglodytes*). Anim Cogn 6:245–251

Tooby J, Cosmides L (2001) Does beauty build adapted minds? toward an evolutionary theory of aesthetics, fiction and the arts. SubStance 30:6–27

VanPool CS, Newsome E (2012) The spirit in the material: a case study of animism in the American Southwest. Am Antiquity 77:243–262

Verpooten J, Nelissen M (2010) Sensory exploitation and cultural transmission: the late emergence of iconic representations in human evolution. Theor Biosci 129:211–221

Weiner J (1994) Aesthetics as a cross-cultural category. Manchester: groups for debates in anthropological theory. Debate held 30th Oct 1993, Muriel Stott Centre, John Rylands University Library of Manchester

Williams GC (1966) Adaptation and natural selection. Princeton University Press, Princeton

Wilson EO (1998) Consilience: the unity of knowledge. Knopf, New York

Zaidel DW, Nadal M, Flexas A et al (2013) An evolutionary approach to art and aesthetic experience. Psychol Aesthet Creat Arts 7:100–109

Part II

Chapter 4: Evolutionary Interactions Between Human Biology And Architecture - Insights From Signaling Theory And A Cross-Species Comparative Approach

General Introduction

Rather than being a recently invented practice, building homes and other architectural constructions, such as temples and monuments, are a perennial part of the human behavioral repertoire, which may have had an important impact on human cultural, genetic, and ecological evolution. Studying architecture from a biological and evolutionary perspective may thus be relevant to the understanding of human evolution; and vice versa, a biological and evolutionary perspective may enhance our understanding of architecture as a crucial part of human life. Yet, human architecture has hardly been investigated from a biological and evolutionary perspective.

In this chapter, we aim to contribute to this much-needed approach to architecture. First, we investigate the evolution of human building aptitudes from a phylogenetic perspective. Then, we address the evolution of aesthetic aspects of architecture and its eventual signaling purposes from a comparative perspective relying on models from signaling theory.

Definitions

Animal building behavior

Building behavior is a kind of construction behavior, like tool making. Whereas it is difficult to non-arbitrarily distinguish tool making from building, construction behavior can be unambiguously defined as follows: “something must be constructed and it must necessitate behavior” (Hansell and Ruxton 2008). For example, coral polyps just secrete coral skeleton, gradually building up reefs, whereas the caterpillar building its pupal defenses employs behavior (Hansell 2007). The basic premise for treating building biology as a single field, a biologically coherent subject, is the biological argument of convergent evolution. In this case, it is that the rules of physics apply universally to all builders and they also share many of the biological hazards in common. Couple this with the fact that there are a limited number of good solutions to any problem and you have a conceptually useful field of study (Hansell, pers. comm.). Since there is no reason to assume that any species would escape the rules of physics, hazards, and logic, this building biology framework should also work for the human species.[8]

Architecture

The New Oxford American Dictionary distinguishes between two meanings of the term architecture. The first interpretation of architecture is "the art or practice of designing and constructing buildings," whereas the second one equates architecture with "the style in which a building is designed or constructed, especially with regard to a specific period, place, or culture, e.g., Victorian architecture." In this chapter, we will address both these aspects of architecture (i.e., 'architecture as building' and 'architecture as the aesthetics of buildings') from an evolutionary and cross-species perspective.

Roles of architecture

Most buildings created by humans are homes. The primary function of homes is to protect humans and their offspring against biotic and abiotic hostile forces, such as (among others) adverse meteorological conditions, predators, or enemy outgroups. Beyond this mere utilitarian function, many buildings are constructed in a specific style: architecture often also has an – intended – aesthetic function, in the sense that many buildings are designed to be perceived. Interestingly, these are also the two main functions of non-human animal constructions. Most of them serve either intraspecific communication, (i.e., displays such as the decorated bowers of bowerbirds), or protection (i.e., nests, trapping function notwithstanding) (Hansell 2005). The argument that will be put forward in this chapter will be built around these two main purposes of human and non-human architecture. In the first section of this chapter, we focus on the protective purposes of buildings, and the evolution of the human building aptitude mainly from a phylogenetic perspective. In the second section, we devote attention to the aesthetic component of

---

[8] In case we would have to conclude that the building biology framework does not apply to humans, it tells us something interesting as well. It would mean that humans are unique in a way that affects human buildings. In such a case, the cross-species perspective on building would help to spell out in what sense humans are unique.

architecture, which we will consider from the perspective of signal evolution. In both these sections, we will investigate the potential interactions between the evolution of building aptitudes, and the signaling functions and the protective functions of architecture throughout evolutionary time.

Building

The origins of human building aptitudes

Did human building aptitudes evolve for the signaling and/or protective purposes which architecture perennially seems to exhibit? Or did they merely emerge from co-option of another aptitude such as tool behavior? To address these questions, it is necessary to take a look at our extant and extinct closest relatives and at the prehistory of Homo sapiens.

Tool behavior is relatively rare in the animal kingdom. The commonly held view is that this is due to the fact that tool behavior is cognitively constrained, i.e., only 'smart' animals are capable of evolving it. However, recently, Hansell and Ruxton (2008) put forward an intriguing alternative explanation for the rarity of tool use. They claim that tools are rare because they are often not useful. In support of their hypothesis, they note that, first, tools are generally not a substantial part of the ecology of species identified as tool users; and, second, tool use has had little evolutionary impact as a driver of speciation, especially in comparison with species that show construction behavior more generally. For example, although crows and finches provide the most numerous examples of tool use in birds, the parrots, noted for their general intelligence, provide few examples of tool use in the wild (Lefebvre et al. 2002). Hansell and Ruxton (2008) suggest as a possible explanation for this that parrots, with their ability to grasp objects in their feet as well as to manipulate them with their beaks, find few circumstances in which a tool would offer an added advantage. In contrast to tools, nests are quite widely distributed in the animal kingdom (Hansell 2005). However, there is no reason to suppose that this is the case because nest building is generally less cognitively constrained than tool behavior. Both can be complex and flexible in some species and stereotyped in other. Rather, nests, in contrast to tools, are very often useful, as they serve the crucial function of protecting builders and their kin against biotic and abiotic hostile forces.

This pattern holds in extant hominids. All great apes routinely build nests, while their tool use is only facultative. Orangutans, for example, do not use tools in the wild (some notable exceptions notwithstanding, see van Schaik 2006). In chimpanzees, tool use seems important as a foraging method only to some chimpanzees at some times of the year (Hansell and Ruxton 2008). However, both species of great apes daily build night nests, and they may even make day nests as well. Chimpanzees are born, spend the majority of their lives, and often die in their nests. One functional aspect of nest building in chimpanzees is that of comfort for sleep, but the functions of chimpanzee nest building are probably multiple (Stewart et al. 2007). Chimpanzee nests are neat, compact, and sturdy structures. Hansell and Ruxton (2008) doubt that the making of a stick tool is cognitively more complex than the making of such a nest.

Sabater Pi et al. (1997) infer from the prevalence of nest building in great apes and from indirect archeological evidence that extinct hominins (e.g., different species of *Australopithecus* and *Homo habilis*) may have been nest builders as well. A speculative proposal is that Homo sapiens inherited this aptitude for building (culturally, genetically, and/or ecologically) from its hominin forebears. Postmoulds, and oval, or circular stone rings may be direct evidence of shelters constructed by Homo species. At any rate, as suggested by Hansell and Ruxton (2008), these findings indicate that nest building may have been a more important factor in the evolution of human construction aptitudes than tool behavior. But what about signaling, the other main function of building in humans and in the animal kingdom? May signaling functions of constructions have played a role in the evolution of human building aptitudes?

With the exception of humans, building for signaling purposes seems virtually absent in the primate lineage. This is surprising since it is safe to assume that, for example, great apes, who construct nests and tools, are cognitively and anatomically perfectly capable of constructing artificial signals. Is it because signaling constructions are for some reason not very useful to non-human primates? The absence of signaling structures in primates stands in stark contrast with the fact that in many bird and fish species artificial signaling is an essential part of their natural behavioral repertoire. Many of these signaling systems are intersexual, but not all (e.g., Sergio et al. 2011). It is an intriguing biological conundrum why humans stand, in this respect, closer to birds and fishes than to their closest non-human relatives.

Considering the widespread human inclination to create signaling structures, humans are the exception to the rule within the primate lineage. As far as is known from the archeological record, the first signaling constructions in the human lineage are artifacts and include adorned tools and complex art such as figurines and rock art. These consistently began to appear from about 35 thousand years ago onwards (Powell et al. 2009).

This brief discussion suggests that the primary evolutionary force in the evolution of human building aptitudes was nest building, while signaling and tool construction co-opted these aptitudes and may have become subsequently secondary forces driving the further elaboration of building in humans.

The biological consequences of building

Material culture is often regarded as a crucial factor in the evolution of intelligence and human ecological dominance. However, as Hansell and Ruxton (2008: 74) point out, "evidence from construction behavior other than that of tool behavior (such as nest building) has tended to be excluded from the debate on the evolution of human intelligence and eco- logical dominance." Yet, the foregoing discussion suggests that nest building has been more common, useful, and potentially as cognitively demanding as tool behavior during human evolution. Therefore, we may expect that, if material culture has impacted the evolution of intelligence and human ecological dominance, it may have been nest building that played a crucial role – and, perhaps to a lesser extent, tool behavior.

The evolution of intelligence

Van Schaik (2006) and others suggest that material culture bootstraps intelligence. If artifacts are useful and if more intelligent individuals can produce more useful artifacts through imitation and invention, a positive evolutionary feedback loop arises between intelligence and material culture. Van Schaik (2006) refers to tools, but following the above reasoning (cf. the section on the Origins of human building aptitudes), nest building may have been at least just as important in this process. And there is an additional reason why it may have been above all nest building rather than tool behavior that has promoted intelligence. Early hominid nesting sites may have created a social environment ideal for exchange of information further bootstrapping intelligence (Fruth and Hohmann 1994). Moreover, one may speculate that in as far as the elaboration of nests or shelters provided ever more protection against hostile forces, the role of active (wakeful) vigilance might have lost some of its importance during sleeping. This further bolstered the evolution of deep sleep, which is known to be a prerequisite for highly complex cognition functioning (Coolidge and Wynn 2006).

Ecological dominance

Since building should assist control over the environment, an association between archi- tectural innovation and extension of habitat range may occur (Hansell 2005). For example, Hölldobler and Wilson

(1990) contend that nest building in some species of weaver ants has significantly contributed to their ecological dominance. Could this be the case for humans as well?

From fur to roof

Human nakedness may have evolved as an adaptation to keep the body cool, which enabled ancestral humans to cover increasingly large foraging distances in the ancestral African savanna. (Wheeler 1984, 1996; Chaplin et al. 1994; Jablonski and Chaplin 2000; Jablonski 2010). Glands that produce watery sweat rather than (ancestral mammalian) oily sweat may have evolved in concert with human nakedness for extra cooling efficiency. If nakedness is an adaptation to keeping cool while running under a burning hot sun, being furless may in turn be unfavorable when the body is inactive, for example during resting. Since all mammals inhabiting the savanna today have fur, except for the exceptionally large ones such as rhino's and elephants, it seems reasonable to suppose that the thermoregulatory function of fur is important – even in a tropical climate. Fur protects against wind and precipitation and helps the organism to keep warm. We speculate that the evolution of nakedness was facilitated by the elaboration of nests replacing the function of fur when being inactive. Great ape nests are relatively simple open constructions. Perhaps, the invention and cultural transmission of a roof construction, which changed the basic great ape nest into a hut-like configuration, was necessary for the functional shift towards nakedness. Based on fossil evidence (i.e., essentially modern body proportions, which would have permitted prolonged walking and running), Jablonski (2010) estimates that the hominin transition to furless- ness may have been well under way by 1.6 million years ago. If our proposal is correct, an elaboration of nest building should have occurred more or less synchronously. However, as discussed above it is very hard at this stage to find any direct evidence of the timing of this shift because shelters and nests would have been mostly made of organic, and hence perish- able, materials.

Out of Africa

Once roofed nest building was in place, it may have contributed significantly to the rapid colonization of other continents. The fact that humans did not grow back fur during or after colonizing habitats with much colder climates is indicative of this. By comparison, mam- moths, which are even bigger than extant elephants, had fur to protect themselves against the cold. Similarly, vultures, whose heads and necks are more or less featherless, have a feathery coat on these body parts in colder climates. It is therefore quite unusual that humans in colder climates did not grow back fur. We suggest that renewed genetic selection for fur may have been dampened by the protection that built structures (i.e., roofed nests or huts) offered. A genetic response to environmental change is usually slower than a cultural one (Boyd and Richerson 1985). In this case, learning and socially transmitting the art of using local materials to build huts dampened the need to grow fur again, which is consistent with (cultural) niche construction theory (Laland and Brown 2006).

Clothes and caves

There are two problems with the from-fur-to-roof proposal: namely, the use of clothes and caves in humans. Regarding caves, one may argue that these are naturally occurring shelters, which may have provided all the necessary protection from biotic and abiotic hostile forces. The availability of caves might thus have made the practice of building huts largely unnecessary. However, while it is indeed the case that caves and other naturally occurring shelters were available to our forebears, there is reason to believe that they were used far more sporadically than commonly assumed. Our ancestors could not only rely on caves for their protection. Since we now know that their lifestyle closely resembles that of contemporary hunter-gatherers, the typical group of ancestral humans probably had to cover large annual foraging distances. They may have had one or more base camps or other sites to which they returned annually, but most of the time they travelled long distances. Culturally maintained knowledge on how to use local materials to build temporary, but high-quality shelters with little effort seems to have been crucial for maintaining that nomadic lifestyle. Moreover, caves which are both accessible and suitable for resting are not that widely distributed in landscapes, nor is their location/entrance very easily detected and remembered. Our ancestors were not the 'cavemen' as the old high school textbooks portrayed them – which is further evidenced by extensive studies of cave sites where remnants of human presence have been found. These studies indicate that these caves were only sporadically used. This is even the case for caves where cave art has been found, leading archeological researchers to postulate that caves were mainly used for ritual purposes, rather than as homes.

Another issue with our from-fur-to-roof proposal relates to the use of clothing. Obviously, clothing can offer important protection against hostile abiotic forces, such as wind, precipitation, and cold. Although clothing may have been a factor in the relaxation of renewed genetic selection for human fur in colder climates, we do not think it made shelters redundant for these protective functions. Yanomami Indians, living in the tropical Amazonas area, for example, do not wear clothes but they use shelters and windscreens (Eibl-Eibesfeldt 2008). Shelters may alternatively be explained as a protective structure against predators, but this does not explain the Yanomamis' use of windscreens. In cold environments, the protection potential of clothing against wind and rain is limited. Especially during sleep, shelters, like huts, may have provided the necessary protection against windy and rainy weather conditions and maintained a relatively stable environmental temperature.

Architectural Aesthetics

Introduction

Signals are designed to be perceived. Since the aesthetic aspects of architecture, just as the aesthetic aspects of any human artifact, are designed to be perceived as well, it is useful to consider them from a signaling perspective. By contrast, awe-evoking sunsets or grand mountain views obviously also appeal to our sense of beauty, but they are not designed for that purpose. Especially, the overall morphology of religious edifices (e.g., the cross-shaped plan of cathedral), which nearly always includes decorations and ornaments, has a clear signaling or communicative purpose rather than only a utilitarian one. In biology, communication and signaling between individuals have been extensively studied, from a theoretical as well as an empirical perspective. Here, we will attempt to demonstrate how these empirical and theoretical findings may shed light on the evolution of aesthetic/signaling aspects of human architecture.

As we have argued in the previous section, signaling was probably relatively unimportant for the initial evolution of human building aptitudes and for the culturally, genetically, and ecologically inherited building practices. However, once the practice of building became established it could have easily been exapted to signaling purposes as well, leading to the emergence of built constructions that served both signaling and directly utilitarian roles (in addition to the existing merely utilitarian constructions), and even constructions that exclusively served signaling purposes, such as monuments. Before addressing the question which particular signaling purposes architecture may serve and why, we give a short review of the main models of signaling theory. After this, we aim to prove these models' relevance for explaining key features and characteristics about human architecture. Three models of signaling theory will be discussed: (a) arbitrary coevolution, (b) sensory exploitation, and (c) costly signaling. These models are mostly applied to explain the evolution of mating traits and mating preferences, and they can be formulated either as complementary (explaining different aspects of signals and their evolution in a given signaling system) or as mutually exclusive mechanisms. There is ongoing discussion about which of these models is the predominant mechanism in intersexual selection. Since they apply, in principle, to any sender–receiver system, including human (cultural) communication systems (Boyd and Richerson 1985), such as architecture, a similar comparative evaluation of these models is relevant in this context.

Arbitrary coevolution

Prum (2010) recently argued that the Lande-Kirkpatrick mechanism – better known as Fisher's runaway process[9] – is the appropriate null model of signal evolution against which alternative models can be comparatively evaluated. In this model, no additional evolutionary forces on either senders or receivers are assumed (i.e., arbitrary coevolution between signalers and receivers). Although developed in the context of intersexual selection, the model applies to aesthetic evolution in general and predicts that arbitrary coevolution oc- curs between aesthetic signals/traits and aesthetic preferences (Prum, pers. comm.). The model thus implies that the aesthetic characteristics of architecture and human preferences for these characteristics are entirely determined by intrinsic factors of the system, i.e., they are evolutionarily neutral.

A number of case studies on human artifacts demonstrate that arbitrary aesthetic evolution can indeed occur. For example, Rogers and Ehrlich's (2008) study suggests that symbolic adornments for Polynesian canoes have no differential effect on survival from group to group. Similarly, Bentley et al. (2007) show that the steady turnover in "pop charts" – including the most popular music, first names, and dog breeds in the 20th-century United States – fits a random copying model. These compelling findings demonstrate that in some cases aesthetic tastes and styles are evolutionarily neutral. Yet, the research question here is whether this arbitrary coevolutionary process applies to aesthetic evolution in general, including architectural styles, or whether it only applies to these local and specific communication systems. Also, one should bear in mind that the aforementioned studies only demonstrate that style or taste differences are arbitrary. This, of course, says nothing about whether the aesthetic signaling system as a whole is evolutionarily neutral or not. Again, consider religious architecture as an example. Stylistic differences between Gothic and Roman architecture may be evolutionarily neutral, while other, shared aesthetic aspects of these styles may not be, for example, their monumentality (see sections on Monumental architecture and costly signaling and Monumental architecture and SE).

[9] The Lande-Kirkpatrick version includes both stable and unstable equilibrium conditions.

Costly signaling

The mechanism

In contrast to the null model, costly signaling (CS) does assume an additional selective pressure external to the context of the signaling system. CS implies direct selection on the senders and, consequently, indirect selection on receivers' responses to the signal. This additional selection on senders is a consequence of a realized cost of the signal. By displaying to being able to bear this handicapping cost, the sender reliably signals its quality. Receivers, on their part, benefit from adjusting their response according to sender quality.

Mostly, a number of criteria are discussed for signals to be counted as handicaps or costly signals. Based on the main handicap results in Grafen's seminal paper (1990), signals can be considered as handicaps if they are (a) honest, (b) costly, (c) and costlier for worse signalers. For example, a recent study showed that a raptor species nest decorations act as reliable signals of viability, territory quality, and conflict dominance of a signaling pair to floating conspecifics (Sergio et al. 2011). By experimentally enhancing nest decorations, researchers showed that in this communication system honesty was maintained by social punishment, which seems to conform to the CS hypothesis (but see Szamado 2011).

Monumental architecture and costly signaling

The mechanism of CS seems particularly relevant to explain religious architectural constructions (e.g., temples, cathedrals). On the one hand, the monumental aspect of such religious buildings appears to serve a signaling rather than a utilitarian function. The domes, towers, or the extraordinarily high ceilings of religious buildings, are of little to no direct practical use. On the other hand, costliness speaks from the fact that a lot of additional effort, resources, and energy go into building monumentally. Given that monumentality is a signal, we would not expect that differences in monumentality are arbitrary to receivers. These observations have led archeological researchers to suggest that religious monuments trans-temporally and cross-culturally evolved because leaders/elites used them to signal their status to commoners and competitors. Specifically, such monumental edifices have been interpreted as 'devices' for vertical stratification, serving to introduce social ranking within communities.

What is the precise mechanism according to which monumental architecture is thought to have fulfilled this socializing role? According to Trigger (1990), such edifices are a clear example of conspicuous consumption (Veblen 1899) because they are largely non-utilitarian and because their construction required massive amounts of energy. By their ability to control that flow of energy and to recruit the labor that was necessary to harness that flow, the (elite) builders – or the ones commanding to construct these buildings – unambiguously demonstrated towards other members of the society that they were the ones that were actually holding power. Non-elites' low social ranking became further underlined by the fact that the elite had the ability to recruit them for participating in building the monumental structure. Or as Trigger (1990: 125) puts it,

[m]onumental architecture and personal luxury goods become symbols of power because they are seen as embodiments of large amounts of human energy and hence symbolize the ability of those for whom they were made to control such energy to an unusual degree. Furthermore, by participating in erecting monuments that glorify the power of the upper class, peasant laborers are made to acknowledge their subordinate status and their sense of their own inferiority is reinforced.

One of the issues with Trigger's account is that it begs the question as to how building non-utilitarian structures could have conveyed an adaptive benefit to the elite builders. Borrowing from the work of Zahavi (1975), Neiman (1998) argues that monumental architecture should be understood as illustrating the handicap principle, i.e., CS. By being able to 'waste' their energy to such buildings, the elite builders reliably signaled to others that they had an excess of power/energy, deterring rival elites to enter into a competition with them. To followers such grand edifices reliably illustrated the elites' qualities as potential leaders. According to Neiman (1998) monumental architecture can thus be viewed as "a form of 'smart advertising,' wherein the signaler accrues the benefits of increased access to labor and resources as a result of paying the cost of construction, and nonsignalers can benefit from associating with more capable elites" (Aranyosi 1999: 357). In the long run, monumental architecture, as an instance of 'wasteful advertising,' gave the elites privileged access over resources and mates, which enhanced their reproductive success. Note that a CS perspective need not necessarily be limited to architectural monumentality per se. Architectural decorations, such as ornamentation, might as well be considered as costly signals. This might be analogous to animal kingdom. For example, red, orange, and yellow carotenoid-dependent ornaments are hypothesized to be a general form of an immunocompetence handicap (Folstad and Karter 1992). The idea is that carotenoids have dual but mutually incompatible roles in immune function and signaling (Lozano 1994). Animals with carotenoid-depended sexual signals are actually demonstrating their ability to 'waste' carotenoids on sexual signals at the expense of their immune system.

Regardless of whether the hypothesis that monumental architecture resulted from CS would prove theoretically and empirically valid or not, it offers an interesting perspective on architecture from a Darwinian and signaling perspective. This is reinforced by the fact that much of what is nowadays known as 'architecture' often has monumental aspects. So, any model trying to attempt to elucidate the evolution and function(s) of monumental architecture from a Darwinian viewpoint goes a long way in explaining some of the function(s) of architecture. It should be noted, however, that there seems to be a near consensus among evolutionary archeologists that a CS explanation suffices to explain monumental architecture. Apart from Joye and Verpooten (2013) (Chapter 6), no attempts have been made to link other signaling models to this building strand. Yet, to avoid the pitfalls of a confirmationist research attitude, CS should be comparatively evaluated against other signaling models. Moreover, regardless of its plausible prevalence in humans, the current methodology may not be suit- able to demonstrate the strategic cost or the wastefulness of the signal, which is a necessary condition for CS (Szamado 2011).

Sensory exploitation

In this section, we explore the sensory exploitation (SE) model (a) as a complementary explanation to CS, and (b) as a true alternative (i.e., mutually exclusive) mechanism for the evolution of monumental architecture. We first introduce the specifics of the SE mechanism. After this, we investigate SE's explanatory potential for monumentality in architecture, as well for other aesthetic properties such as decorative and compositional elements in architecture.

The mechanism

Sensory exploration is a model that is increasingly receiving attention (e.g., Ryan 1998; Arnqvist 2006). Central to SE is that senders evolve display traits to exploit pre-existing biases of receivers,[10] or biases that are under strong selective pressure in another context than the SE system such as perceptual biases adapted for fi nding food or avoiding becoming food. These male traits may often be costly, but that does not necessarily mean that they reliably correlate with quality, which is a requirement to regard the trait as a costly signal. In recent years, theoretical evidence (see Fuller, Houle and Travis 2005) as well as empirical

---

[10] Usually the term sensory exploitation is interpreted quite broadly, referring not only to the exploitation of sensory biases, but also to the exploitation of receivers' emotional and cognitive biases. Moreover, biases do not need to be innate but can be learned as well, given that they are maintained by strong functionality outside the signaling context. Therefore, sometimes the more inclusive term *receiver psychology* is used.

evidence (see Rodriguez and Snedden 2004) for the role of SE in sexual selection has been steadily accumulating, establishing it as a valuable alternative to CS.

Take, for the sake of comparison with CS, again the example of colorful signals that are carotenoid-dependent. SE suggests an alternative explanation for the female preference for red, orange, and yellow carotenoid-dependent ornaments. Rather than being an indicator of male quality, they may be mimicking signals to which females are biased. In support of SE, Rodd et al. (2002) indeed found evidence that female guppies' (*Poecilia reticulata*) preference for males with larger, more chromatic orange spots results from a sensory bias for the color orange, which might have arisen in the context of food detection. With respect to animal built constructions, relevant in this context, similar fi ndings have been made. Madden and Tanner (2003) found that some species of bowerbirds prefer to eat fruit of a similar color to the decorations found on their bowers.

Some studies offer clear evidence of SE as a true alternative to costly signaling (CE). For example, in a well-documented case, male water mites mimic prey in order to attract the attention of females (Proctor 1991, 1992). This case illustrates the strong version of SE because it precludes CS to operate. CS requires signal receivers to choose on the basis of perceived quality, whereas here females are clearly tricked and are thus unable to exert any choice. Notice, however, that SE and CS are not necessarily mutually exclusive, although theoretically they can be formulated as such (Fuller et al. 2005). There also exist weaker versions of SE theory that may complement models like CS. They commonly explain specific aspects of costly signal evolution, for example, why a costly signal takes on a specific wasteful form rather than another one. This weaker version of SE is commonly called *sensory drive*, and it focuses on aspects such as signal efficiency (Endler 1992). Often, however, a clear distinction between sensory drive and SE is unwarranted, and usually these theoretical variants are lumped together. The strong version of SE differs from the null model in the same way it differs from CS in that it precludes coevolution between senders and receivers. Applied to architecture, this means that if it were shown that human responses to architecture are largely determined by preferences that are/were selected in another context, rather than by coevolution with architectural styles (which, whether CS or not, i.e., arbitrary coevolution, refer to a quality of the sender), this would qualify as evidence that SE is the main mechanism underlying the evolution of architectural aesthetics.

Exploitation of human biases in architecture

Many studies suggest that humans experience an adaptive lag, that is, a mismatch between current selection pressures and behavior (Laland and Brown 2006). For example, humans have a biologically prepared fear for archaic dangers, such as snakes or spiders, but they do not have such prepared fears for modern threats like cars (Marks and Nesse 1994). Evolutionary psychologists, such as Cosmides and Tooby (1987: 280–281) give the following description of this mismatch:

> [t]he recognition that adaptive specializations have been shaped by the statistical features of ancestral environments is especially important in the study of human behavior. … Human psychological mechanisms should be adapted to those environments, not necessarily to the 20th-century industrialized world.

Laland and Brown (2006) contend that, while it is a truism that any animal, including humans, experiences some adaptive lag, the mismatch between an animal and its environment is generally compensated by niche-constructing activity. We assume that SE is one of the mechanisms through which niche construction is obtained and selection against archaic biases dampened. We propose that architectural environments, which are part of the constructed human niche, are shaped by the exploitation of these archaic adaptive human biases. This exploitation process may – in principle – be neutral, beneficial, or maladaptive to human receivers. To stick with the example of the maladaptive lack of fear of cars, it might be no coincidence that BMW's have "angry" face-like fronts (Windhager et al. 2011). This can signal that these cars are in fact relatively more dangerous to vulnerable road users than average cars. Or at least, it may assist BMW users in scaring away road users that may slow them down. Similarly, we expect that utilitarian buildings may acquire signaling features as a result of SE. In the following sections, we speculate about the kinds of pre-existing human perceptual, cognitive, and/or emotional biases that may become exploited in architecture, and about the functions – if any – they serve.

Architectural compositions and decorations

There have been a few attempts to approach architectural aesthetics from an evolutionary perspective. One such perspective takes habitat theory as its starting point,[11] which was originally proposed by Orians

[11] Note that there are other uses of the term habitat theory.

and Heerwagen (1992). This perspective can be accommodated to the SE framework, which in turn allows comparative evaluation with other models. Central to habitat theory is the assumption that the human species has 'inborn' (aesthetic) preferential biases for particular landscape features and/or organizations, and elements that were invariably present in ancestral environments (e.g., animal life, water features). Preferential biases for these features/organizations and elements are claimed to be evolved adaptations. They increased genetic fitness by enhancing the probability that ancestral humans would explore environments which offered them sufficient opportunities for protection (e.g., against predators, weather), and which guaranteed the availability of resources. These preferential biases are claimed to be present in architecture.

Within this context, it has been proposed that humans have a preferential bias for parklike or savanna-type environments (Orians and Heerwagen 1992). These environments are sometimes believed to be the environments in which humans evolved. Among other characteristics, savanna-type environments are relatively open, have a fairly even ground surface, are only moderately complex, and contain relatively high levels of biomass (Orians and Heerwagen 1992; Ulrich 1983). An evolved (aesthetic) preferential bias for environmental features or configurations typical to this biome made that early humans were drawn to environments where potential dangers (e.g., predators) could be seen from quite a distance, where locomotion was relatively easy and unimpeded, and which offered opportunities to "see without being seen" (cf. Appleton 1975).

In recent years some scholars have used the previous research findings to explain particular aspects about the aesthetics of architecture and the built environment (Joye 2007; Hildebrand 1999; Kellert 2005). The argument is that when humans are freely left to organize their living environments in a way which feels comfortable to them, they are inclined to integrate these preferential biases into architectural design because these features reflect a "good habitat." Constructing built environments/habitats that appeal to our senses should thus reflect these evolved preferential biases. For example, the fact that people like dwellings offering a broad and unimpeded view on the surrounding environment or prefer intermediately complex environments has been interpreted as a reflection of these biases, and specifically of the savanna bias (Appleton 1975).

The fact that cities and buildings do not directly resemble savannas (except for their parks, perhaps) may be seen as a problem for the hypothesis that they mimic a savanna environment. However, this hypothesis only states that the bias for such an environment would be (architecturally) expressed if humans were freely left to choose. Therefore, a plausible reason for the lack of savanna-like features in human-built surroundings may be that we are just not often in a position to choose. To put it in more mechanistic terms, this kind of SE is probably often overridden by stronger selective pressures, such as the need for protection from current biotic and abiotic hostile forces.

Perhaps a more serious challenge for this 'savanna hypothesis' is the human behavioral ecology view that humans evolved as opportunistic ecological generalists in variable environments (Smith and Wishnie 2000). As a result, humans are behaviorally flexible and can accommodate themselves to a wide range of circumstances and habitats (Smith, Borgerhoff Mulder and Hill 2001), It seems, however, that a significant part of this accommodation is achieved through niche construction (instead of behavioral flexibility), which in turn negates modifying selection on pre-existing biases (Odling-Smee et al. 2003). In turn, this would then favor the savanna hypothesis. Yet, the claim for a human-evolved preference for savanna-like environments remains relatively speculative claim given that our human ancestors also lived in other types of biomes, both before and after dwelling the African savanna.

A more convincing case of SE in architecture can perhaps be made if we consider the elements that have been invariably present across the range of possible habitats human ancestors have inhabited and that were especially relevant to their survival. It seems that above all the category of 'living things' seems to qualify, specifically animals (including conspecifics), and vegetative life. It is a truism that during human evolution negotiating successfully with animals – either predator or prey – as well as the ability to locate and gather foods of vegetal origin (e.g., roots, flowers, berries, and herbs) were of crucial importance to human survival. Given these selective pressures, it has been claimed that humans evolved a number of (affectively guided) detection, recognition and memory mechanisms (Barrett 2005). Consistent with this, experimental research supports the claim for the existence of domain-specific cognitive (i.e., attentional, memory) and emotional mechanisms to deal with the category of living things. For example, children already at a very young age are able to make a differentiation between (crucial features differentiating) animate and nonanimate categories (Gelman and Opfer 2002). Neuropsychological research into so-called "category specific deficits" points to the existence of domain-specific neural areas that are specialized in storing knowledge about living/animate entities (e.g., animals, vegetative life; cf. Caramazza and Shelton 1998).

Regarding the category 'plant life,' females seem to have a number of cognitive advantages over males, possibly refl ecting an evolved/ancient division of labor (i.e., females as gatherers, males as hunters). For example, Neave and colleagues (2005) found that females are quicker than males in recognizing plant targets and in remembering the location of those targets (for similar results, see Schussler and Olzak 2008). Research also indicates a female, as opposed to a male, advantage for location memory for fruits (New and Krasnow et al. 2007; Krasnow et al. 2011). Data from semantic knowledge studies point out that females have an advantage to males for knowledge about plant categories (Laiacona et al. 2006).

With regard to animal life it has been shown that neurons in the right amygdala respond preferentially to pictures of animals, which might refl ect the evolutionary signifi cance of this category of animates (Mormann et al. 2011). Pratt and colleagues (2010) found that animate motion captures visual attention more readily than inanimate motion. New, Cosmides and Tooby (2007) report that respondents are faster and more accurate in detecting changes to scenes containing animals than to scenes with inanimate objects such as vehicles. Eye movement studies show that respondent are more likely to attend to animals than to objects, and animals are also attended longer in time than objects (Yang et al. 2012). Of further importance is that lesion studies show that males are more likely to become impaired for knowledge about plant life than about animals. Scotti et al. (2010) argue that factors other than familiarity need to be taken into account to explain this animal advantage. Specifically, they speculate that this pattern refl ects males' role as hunters in ancestral times.

Our SE perspective on aesthetics predicts that these pre-existing and strong adaptive biases for living things can become exploited in architectural constructions. The fact that across all human cultures there is a perennial tendency to adorn architecture with ornamental elements that refer to the animal kingdom and/or that bear close resemblance with botanical elements (e.g., flowers, fruit) seems to support this prediction. And indeed, studies such as Windhager et al.'s (2011), in which it was found that in a real-life setting (window displays in a mall) the presence of animal life is found to lead to increased attention and exploration, suggest that these universally human adornments of architecture effectively evolved by exploiting human biases for living things.

We have discussed the attention-grabbing potential of architecture in which life-like elements are integrated. Living things, however, may grab attention for two quite distinct reasons: fi nding food, and avoiding becoming food. As a consequence, this process is mediated by either positive or negative emotional responses, respectively. This is somewhat neglected by evolutionary psychologists, who tend to focus on preferences in the context of art. For example, Pinker (1997) argues that art evolved by pushing human "pleasure-buttons." We believe, however, that both negative and positive emotions have played a role in the evolution and propagation of art. Pleasure may be an important proximate mechanism mediating the SE process, leading to “aesthetically pleasing” architectural features. However, we do not think it is the only proximate mechanism mediating the evolution of art. Aversive emotions, such as fear and disgust, are much stronger than positive emotions, such as joy, which makes sense given their adaptive signifi cance in life-threatening situations. Stronger biases are easier triggered, and therefore we can assume that – all else being equal – they have a higher chance of being exploited by artifi cial elicitors. This may lead to a lasting incorporation of these artifi cial elicitors in the culturally and ecologically maintained environment of which architecture is part. Consider some fear-evoking features of buildings, such as pointy spires, which may mimic teeth, or monumental heights, inducing anxiety or submissiveness in observers, etc. These features may be experienced as aesthetically grasping because they attract otherwise adaptive attention, and they may lead to an intense emotional experience because the body is preparing itself for ‘fi ght or fl ight.’ In the past, institutions have indeed employed frightening features/elements for signaling dominance and for inducing obedience and/or compliance in community members (e.g., in Gothic cathedrals?).

In the following sections, we discuss a potential ultimate function of SE by (means of) monumental architecture. Specifi cally, we claim that by exploiting awe – which is an intriguing mixture of positive and negative emotions, and a common response to monumentality – monumental architecture ultimately served social organization within and across communities. However, it may also be that frightening architectural features get propagated for no purpose at all. They may persist and get culturally copied just because they grasp attention. For example, highly disgusting stories are found to more readily spread in a population of social learners than less disgusting stories (Heath, Bell and Sternberg 2001). Through a similar process of negative emotional selection, architectural features may get propagated across time and space. While architecture can thus exhibit aesthetic features through ‘purposeless’ SE, this begs the question as to why not all human-built constructions exhibit aesthetic features exploiting such biases. In modern societies, buildings are often merely utilitarian and are entirely devoid of all possible aesthetic features (consider the large suburban apartment blocks built for the ever-growing population of urban dwellers). Probably, this is due to the fact that SE can be overridden by the function of providing protection against biotic and abiotic hostile forces.

Monumental architecture and SE

As complementary to CS

Neiman's (1998) CS perspective says that particular aesthetic attributes about architecture fulfill(ed) an adaptive function for their elite builders and the commoners that perceived them. However, as pointed out elsewhere (Joye and Verpooten 2013; Chapter 6), if it is assumed that CS indeed plays a role, it can only partially explain the (evolved) function of monumental architecture. Specifically, it remains silent about the question why the waste of (building) energy has systematically become concentrated into a particular monumental building form. It seems that many monumental structures derive their monumentality in large part from the fact that they are very high, and/or contain visual cues which further accentuate that height (e.g., vertical features). But if wasting energy is the primary thing that matters, why did the elites invest their available energy in building one high building form rather than in – say – a range of smaller buildings? This question is far from trivial, and it points out that the formal appearance of monumental architecture also contributes to its proposed social function.

In both human and non-human animals, the perception or presence of cues indicative of large size – such as height or verticality – is associated with and power/dominance. This so-called *bias for bigness* speaks from different behaviors. For example, during dominance displays in non-human primates, the dominant animal (or the one trying to dominate) creates impressions of dominance through grandstanding or other bodily changes (e.g., piloerection) (De Waal 1982). In humans, making oneself taller, adopting wide and "open" body positions (Huang et al. 2011), or standing on an elevation (Schwartz et al. 1982) increase perceptions of dominance and power and even cause submissive behavior in observers (Tiedens and Fragale 2003). Important to our account is that similar effects are obtained with simple verticality or size cues. Judgments about power/dominance are often framed as differences in vertical space, where a high ('up') versus low ('down') vertical position are associated with the powerful versus powerless, respectively (see e.g., Schubert 2005; Giessner and Schubert 2007; Moeller et al. 2008).

We contend that monumental architecture exploits the bias to associate height, size and verticality cues with power/dominance, and, in so doing, contributes to vertical social strati- fi cation. Analogous to a (human or non-human) individual performing a dominance display, monumental architecture forces the observer into submission, or at least attempts to instill feelings of inferior social ranking. According to this view, the actual appearance/gestalt of the edifi ce, and not solely the recognition of the energy invested in the building process, furthered monumental architecture's social role. Note furthermore that inasmuch as monumental architecture is a signal of prestige, such edifi ces might have also motivated people to attach to the dominant group/authority that is embodied in these buildings (Henrich and Gil-White 2001).

Because of their massive scale, instances of monumental architecture probably very intensely stimulate the proposed bias for bigness. When this happens, the emotion of awe might become triggered because awe is a common emotional response to stimuli that are characterized by overwhelming vastness (Keltner and Haidt 2003). Paralleling the effects of perceiving the bias for bigness, experiencing awe makes individuals more prone to feel submissive toward the individual/institution causing this emotion, and it can spark sentiments of smallness/nothingness. Note, however, that if monumental architecture indeed causes awe, then this might reveal an additional social function of such architecture (apart from vertical stratification). Empirical research shows that awe leads to feelings of oneness with others (Van Cappellen and Saroglou 2012), makes people identify with a larger group (Shiota et al. 2007), and makes them feel more connected and committed to others (Saroglou et al. 2008). One of the possible mechanisms is that through its grandeur, monumental architecture shakes individuals' mental structures and causes feelings of (cognitive) insignifi cance in them, with the result that people are inclined to 'fl ock together' as a way to compensate for those feelings. An SE perspective on monumental architecture can thus reveal additional social functions of this building strand.

An alternative to CS

The CS account of monumental architecture is not without problems. On the ground of empirical data and theoretical considerations, it may be useful to consider alternative explanations, based on SE, for example, as well.

As discussed at length in the section on CS (see the section on costly signaling), CS can only operate if a number of conditions are fulfilled. One condition is that the wastefulness of the signal needs to be a reliable indicator of a hidden quality of the sender. In the case of monumental architecture, this means that there must be a correlation between the leader's quality and the monumentality of the construction. A problem to the CS account of monumental architecture is that this correlation emerges from receivers comparatively evaluating signalers before making a choice. That is, commoners must be able to compare monuments of different potential leaders before choosing whom to follow – much like female bowerbirds visit and inspect several bowers of males before deciding with which one to mate (Madden 2003). This is the only possible way for the evolutionary establishment of the link between the signal and the hidden quality. Of course, this does not seem to be a very plausible scenario for commoners. Once born in a society, a commoner would most likely have stayed in that society, without ever being exposed to the monuments of the leaders of other communities.

If this argument is correct, CS is precluded as the mechanism underlying the function of monumental architecture because it requires from commoners a free comparative evaluation of the leaders' monumental accomplishments. While it seems plausible that style differences in monumental architecture have no differential effect on survival from group to group (cf. Rogers and Ehrlich 2008; cf. the arbitrary coevolution model outlined in the section on arbitrary coevolution), it is unlikely that the monumentality of the religious buildings itself stems from an arbitrary coevolutionary process. Instead, there must have been a selection pressure that stably pushed religious architecture in this direction across different cultures and epochs.

If it is not CS and arbitrary coevolution that drives monumentality, does it make sense to turn to SE as the only viable explanation? At the very least, we may speculate that SE does more than merely complement CS with respect to religious monumental architecture, and that it may even be possible to formulate it as a true alternative explanation to CS. As we have seen in the section elucidating the mechanism of SE, the prerequisite for SE to occur is that the receivers' choice is precluded because they are tricked. Might monumental architecture as well function as a perceptual trap that tricks human receivers? At least two possibilities are conceivable.

First, we could stick to Trigger's (1990) and Neiman's (1998) view that leaders indeed use their power over commoners and resources to construct monumental buildings. But instead of reliably signaling their hidden – in Neiman's (1998) account, genetic – quality by a costly signal, they trick commoners by overpowering them with the awe-invoking appearance of their monuments.

A second alternative hypothesis that might be worth exploring is the idea that monumental architecture evolved as a consequence of some form of self-exploitation. Self-exploitation is a specific case of SE in which senders are – by accident – receivers as well (Verpooten and Nelissen 2010; Chapter 7). For example, male fiddler crabs are attracted to their own courtship constructions (Ribeiro et al. 2006). Similarly, it may be that commoners act both as senders and receivers of the signaling system; they may have been actively participating in building public monuments merely as a result of the awe-experience such monuments induced. Under this scenario, the monuments get propagated by a form of emotional selection (cf. Heath et al. 2001). We have only briefly hinted at two possible alternative hypotheses for monuments based on the mechanism of SE. However, we think that given the explanatory power of SE in signaling evolution, it deserves further exploration with respect to this specific communication system as well.

Conclusions

In this chapter, we deployed a biological and evolutionary perspective to human architectural accomplishments. We distinguished and investigated two main purposes of architecture: a protective function, and a signaling function. Based on a phylogenetic approach, we speculated that the protective function of architecture has been the main selection pressure on the evolution of human building aptitudes, which in turn may have promoted the evolution of human intelligence and ecological dominance. Contrary to other primate genera, these building aptitudes were, at a later stage in the evolution of Homo co-opted for artificial signaling, which can also be found in other species, especially in fish and birds. We comparatively evaluated three models of signal evolution with respect to architectural aesthetics employing a special focus on monumental architecture. Although at this stage our approach may not allow drawing any definitive conclusions, we hope that the pluralistic biological and evolutionary perspective we explored will prove fruitful for further investigations of the biological and evolutionary relevance of human architecture.

References

Appleton, J. (1975) *The Experience of Landscape.* New York: Wiley.

Aranyosi, E.F. (1999) Wasteful advertising and variance reduction: Darwinian models for the significance of nonutilitarian architecture. *Journal of Anthropological Archaeology* 18, 356–375.

Arnqvist, G. (2006) Sensory exploitation and sexual conflict. *Philosophical Transactions of the Royal Society of London, Series B* 361, 375–386.

Barrett, H.C. (2005) Adaptations to predators and prey. In D.M. Buss (ed.) *The Handbook of Evolutionary Psychology.* New York: Wiley, 200–223.

Bentley, R.A., Lipo, C.P., Herzog, H.A., Matthew, W. and Hahn, M.W. (2007) Regular rates of popular culture change refl ect random copying. *Evolution and Human Behavior* 28, 151–158.

Boyd, R. and Richerson, P.J. (1985) *Culture and the Evolutionary Process.* Chicago: University of Chicago Press.

Caramazza, A. and Shelton, J.R. (1998) Domain-specific knowledge systems in the brain: The animate–inanimate distinction. *Journal of Cognitive Neuroscience* 10, 1–34.

Chaplin, G., Jablonski, N.G. and Cable, N.T. (1994). Physiology, thermoregulation and bipedalism. *Journal of Human Evolution* 27, 497–510.

Coolidge, F.L. and Wynn, T. (2006) The effect of the tree-to-ground sleep transition in the evolution of cognition in early Homo. *Before Farming: The Anthropology and Archaeology of Hunters-Gatherers* 2, 1–16.

Cosmides, L. and Tooby, J. (1987) From evolution to behavior: Evolutionary psychology as the missing link. In: J. Dupré (ed.) *The Latest on the Best: Essays on Evolution and Optimality.* Cambridge, MA: MIT Press.

de Waal, F.B.M. (1982) *Chimpanzee Politics: Power and Sex among Apes.* London: Jonathan Cape.

Eibl-Eibesfeldt, I. (2008) *Weltsprache Kunst: Zur Natur- und Kunstgeschichte bildlicher Kommunikation.* Brandstätter Verlag.

Endler, J.A. (1992) Signals, signal conditions, and the direction of evolution. *The American Naturalist* 139, 125–153.

Folstad, I. and Karter, A.J. (1992) Parasites, bright males, and the immunocompetence handicap. *American Naturalist* 139, 603–622.

Fruth, B. and Hohmann, G. (1994) Nest building behaviour in the great apes: The great leap forward? In: W.C. McGrew et al. (eds.) *Great Ape Societies.* Cambridge: Cambridge University Press, 225–240.

Fuller, R.C., Houle, D. and Travis J. (2005) Sensory bias as an explanation for the evolution of mate preferences. *American Naturalist* 166, 437–446.

Gelman, S.A. and Opfer, J.E. (2002) Development of the animate–inanimate distinction. In: U. Goswami (ed.) *Blackwell Handbook of Childhood Cognitive Development.* Oxford, UK: Blackwell, 151–166.

Giessner, S.R. and Schubert, T.W. (2007) High in the hierarchy: How vertical location and judgments of leaders' power are interrelated. *Organizational Behavior and Human Decision Processes* 104, 30–44.

Grafen, A. (1990) Biological signals as handicaps. *Journal of Theoretical Biology* 144, 246–517.

Hansell, M. and Ruxton, G.D. (2008) Setting tool use within the context of animal construction behaviour. *Trends in Ecology and Evolution* 23, 73–78.

Hansell, M.H. (2005) *Animal Architecture.* Oxford: Oxford University Press.

Hansell, M.H. (2007) *Built by Animals. The Natural History of Animal Architecture.* Oxford: Oxford University Press.

Heath, C., Bell, C. and Sternberg, E. (2001) Emotional selection in memes: The case of urban legends. *Journal of Personality and Social Psychology* 81, 1028–1041.

Henrich, J. and Gil-White, F.J. (2001) The evolution of prestige: Freely conferred status as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior* 22, 165–196.

Hildebrand, G. (1999) *Origins of Architectural Pleasure.* Berkeley, CA: University of California Press.

Hölldobler, B. and Wilson, E.O. (1990) *The Ants.* Berlin: Springer-Verlag.

Huang, L., Galinsky, A.D., Gruenfeld, D.H. and Guillory, L.E. (2011) Powerful postures versus powerful roles: Which is the proximate correlate of thought and behavior? *Psychological Science* 22, 95–102.

Jablonski, N.G. (2004) The evolution of human skin and skin color. *Annual Review of Anthropology* 33, 585–623.

Jablonski, N.G. (2010) The naked truth: Why humans have no fur. *Scientifi c American* 302, 28–35.

Jablonski, N.G. and Chaplin, G. (2000). The evolution of human skin coloration. *Journal of Human Evolution* 39, 57–106

Joye, Y. (2007) Architectural lessons from environmental psychology: The case of biophilic architecture. *Review of General Psychology* 11, 305–328.

Joye, Y. and Verpooten, J. (2013) An exploration of the functions of religious monumental architecture from a Darwinian perspective. *Review of General Psychology*, 53–68.

Kellert, S. (2005) *Building for Life: Understanding and Designing the Human-Nature Connection.* Washington, DC: Island Press.

Keltner, D. and Haidt, J. (2003) Approaching awe, a moral, spiritual, and aesthetic emotion. *Cognition and Emotion* 17, 297–314.

Krasnow, M.M., Truxaw, D., Gaulin, S.J., New, J., Ozono, H. and Uono, S. et al. (2011) Cognitive adaptations for gathering-related navigation in humans. *Evolution and Human Behavior* 32, 1–12.

Laiacona, M., Barbarotto, R. and Capitani, E. (2006) Human evolution and the brain representation of semantic knowledge: Is there a role for sex differences? *Evolution and Human Behavior* 27, 158–168.

Laland, K.N. and Brown, G.R. (2006) Niche construction, human behavior, and the adaptive-lag hypothesis. *Evolutionary Anthropology* 15, 95–104.

Lefebvre, L., Nicolakakis, N. & Boire, D. (2002) *Tools and Brains in Birds. Behavior* 139, 939–973.

Lozano, G.A. 1994. Carotenoids, parasites, and sexual selection. *Oikos* 70, 309–311.

Madden, J.R. (2003) Bower decorations are good predictors of mating success in the spotted bowerbird. *Behavioral Ecology and Sociobiology* 53, 269–277.

Madden, J.R. and Tanner, K. (2003) Preferences for coloured bower decorations can be explained in a nonsexual context. *Animal Behavior* 65, 1077–1083.

Marks, I.M. and Nesse, R.M. (1994) Fear and fi tness: An evolutionary analysis of anxiety disorders. *Ethology and Sociobiology* 15, 247–261.

Moeller, S.K., Robinson, M.D. and Zabelina, D.L. (2008) Personality dominance and preferential use of the vertical dimension of space: Evidence from spatial attention paradigms. *Psychological Science* 19, 355–361.

Mormann, F., Dubois, J., Kornblith, S., Milosavljevic, M., Cerf, M. and Ison, M. et al. (2011) A categoryspecifi c response to animals in the right human amygdala. *Nature Neuroscience* 14, 1247–1249.

Neave, N., Hamilton, C., Hutton, L., Tildesley, N. and Pickering, A. (2005) Some evidence of a female advantage in object location memory using ecologically valid stimuli. *Human Nature* 16, 146–163.

Neiman, F. (1998) Conspicuous consumption as wasteful advertising: A Darwinian perspective on spatial patterns in Classic Maya terminal monument dates. In: C.M. Barton and G.A. Clark (eds.) *Rediscovering Darwin: Evolutionary Theory in Archaeological Explanation.* Arlington: American Anthropological Association, 267–290.

New, J., Cosmides, L. and Tooby, J. (2007) Category-specifi c attention for animals refl ects ancestral priorities, not expertise. *Proceedings of the National Academy of Sciences* 104, 16598–16603.

New, J., Krasnow, M.M., Truxaw, D. and Gaulin, S.J. (2007) Spatial adaptations for plant foraging: Women excel and calories count. *Proceedings of the Royal Society B: Biological Sciences* 274, 2679–2684.

Odling-Smee, F.J., Laland, K.N. and Feldman, M.W. (2003) *Niche Construction: The Neglected Process in Evolution.* Monographs in Population Biology 37. Princeton: Princeton University Press.

Orians, G.H. and Heerwagen, J.H. (1992) Evolved responses to landscapes. In: J.H. Barkow, L. Cosmides and J. Tooby (eds.) *The Adapted Mind: Evolutionary Psychology and the Generation of Culture.* New York: Oxford University Press, 555–579.

Pinker, S. (1997) *How the Mind Works.* New York: Norton.

Powell, A., Shennan, S. and Thomas, M.G. (2009) Late Pleistocene demography and the appearance of modern human behavior. *Science* 324, 1298–1301.

Pratt, J., Radulescu, P., Guo, R.M. and Abrams, R.A. (2010) It’s alive! Animate motion captures visual attention. *Psychological Science* 21, 1724–1730.

Proctor, H.C. (1991) Courtship in the water mite *Neumania papillator:* Males capitalize on female adaptations for predation. *Animal Behavior* 42, 589–598.

Proctor, H.C. (1992) Sensory exploitation and the evolution of male mating behaviour: A cladistic test using water mites *Acari Parasitengona. Animal Behavior* 44, 745–752.

Prum, R.O. (2010) The Lande–Kirkpatrick mechanism is the null model of evolution by intersexual selection: Implications for meaning, honesty, and design in intersexual signals. *Evolution* 64 (11), 3085–3100.

Ribeiro P.D., Christy J.H., Rissanen R.J. and Kim T.W. (2006) Males are attracted by their own courtship signals. *Behavioral Ecology and Sociobiology* 61, 81–89.

Rodd, F.H., Hughes, K.A., Grether, G.F. and Baril, C.T. (2002) A possible non-sexual origin of a mate preference: Are male guppies mimicking fruit? *Proceedings of the Royal Society of London Series B* 269, 475–481.

Rodriguez, R.L. and Snedden, W. (2004) On the functional design of mate preferences and receiver biases. *Animal Behavior* 68, 427–432.

Rogers, D. and Ehrlich, P. (2008) Natural selection and cultural rates of change. *PNAS* 105, 3416–3420.

Ryan, M.J. (1998) Sexual selection, receiver biases, and the evolution of sex differences. *Science* 281, 1999–2003.

Sabater Pi, J., Vea, J.J. and Serrallonga, J. (1997) Did the fi rst hominids build nests? *Current Anthropology* 38, 914–916.

Saroglou, V., Buxant, C. and Tilquin, J. (2008) Positive emotions as leading to religion and spirituality. *Journal of Positive Psychology* 3, 165–173.

Schubert, T. (2005) Your Highness: Vertical positions as perceptual symbols of power. *Journal of Personality and Social Psychology* 89, 1–21.

Schussler, E.E. and Olzak, L.A. (2008) It's not easy being green: Student recall of plant and animal images. *Journal of Biological Education* 42, 112–118.

Schwartz, B., Tesser, A. and Powell, E. (1982) Dominance cues in non-verbal behavior. *Social Psychology Quarterly* 45, 114–120.

Scotti, S., Laiacona, M. and Capitani, E. (2010) Brain damage and semantic category dissociations: Is the animals category easier for males? *Neurological Sciences* 31, 483–489.

Sergio, F., Blas, J., Blanco, G., Tanferna, A., López, L., Lemus, J.A. and Hiraldo, F. (2011) Raptor nest decorations are a reliable threat against conspecifi cs. *Science* 331, 327–330.

Shiota, M., Keltner, D. and Mossman, A. (2007) The nature of awe: Elicitors, appraisals, and effects on self-concept. *Cognition and Emotion* 21, 944–963.

Smith, E.A. and Wishnie, M. (2000) Conservation and subsistence in small-scale societies. *Annual Review of Anthropology* 29, 493–524.

Smith, E.A., Borgerhoff Mulder, M. and Hill, K. (2001) Controversies in the evolutionary social sciences: A guide for the perplexed. *Trends in Ecology and Evolution* 16, 128–135.

Stewart, F., Pruetz, J. and Hansell, M. (2007) Do chimpanzees build comfortable nests? *American Journal of Primatology* 69, 930–939.

Szamado, S. (2011) The cost of honesty and the fallacy of the handicap principle. *Animal Behavior* 81, 3–10.

Tiedens, L.Z. and Fragale, A.R. (2003) Power moves: Complementarity in dominant and submissive nonverbal behavior. *Journal of Personality and Social Psychology* 84, 558–568.

Trigger, B.G. (1990) Monumental architecture: A thermodynamic explanation of symbolic behaviour. *World Archaeology* 22, 119–132.

Ulrich, R.S. (1983) Aesthetic and affective response to natural environment. In: I. Altman and J.F. Wohlwill (eds.) *Human Behavior and the Environment.* Vol. 6. New York: Plenum Press, 85–125.

van Cappellen, P. and Saroglou, V. (2012) Awe activates religious and spiritual feelings and behavioral intentions. *Psychology of Religion and Spirituality.* (Forthcoming.)

van Schaik, C. (2006) Why are some animals so smart? The unusual behavior of orangutans in a Sumatran swamp suggests a surprising answer. *Scientific American* 294, 64–71.

Veblen, T. (1899/1994) *The Theory of the Leisure Class.* New York: Penguin Books.

Verpooten J. and Nelissen M. (2010) Sensory exploitation and cultural transmission: The late emergence of iconic representations in human evolution. *Theory in Biosciences* 129, 211–221.

Webster, D. and Kirker, J. (1995). Too many Maya, too few buildings: Investigating construction potential at Copan, Honduras. *Journal of Anthropological Research* 51, 363–387.

Wheeler, P.E. (1984). The evolution of bipedality and loss of functional body hair in hominids. *Journal of Human Evolution* 13, 91–98.

Wheeler, P.E. (1996). The environmental context of functional body hair loss in hominids (a reply to Amaral, 1996). *Journal of Human Evolution* 30, 367–371.

Windhager, S., Atzwanger, K., Bookstein, F.L. and Schaefer, K. (2011) Fish in a mall aquarium: An ethological investigation of biophilia. *Landscape and Urban Planning* 99, 23–30.

Yang, J., Wang, A., Yan, M., Zhu, Z., Chen, C. and Wang, Y. (2012) Distinct processing for pictures of animals and objects: Evidence from eye movements. *Emotion.* Advance online publication. doi: 10.1037/a0026848.

Zahavi, A. (1975) Mate selection: A selection for a handicap. *Journal of Theoretical Biology* 53, 205–214.

Chapter 5: Architectural Aesthetics, Emotions And Cultural Evolution

Introduction

The behavioral repertoire of humans – unlike that of most nonhuman animals – relies heavily on social learning (Henrich & McElreath, 2003), which has conferred considerable adaptive advantages. Specifically, the capacity to accumulate and retain locally adaptive cultural innovations has enabled humans to spread around the globe and occupy a larger range than any other terrestrial vertebrate (Boyd, Richerson & Henrich 2011). Apart from culturally adapting to new environments, niche construction theory captures the fact that humans also actively modify their environment, which in turn feeds back on cultural and genetic evolution (Odling-Smee, 2010). In humans, as in many other animals, architecture (i.e., structures built mainly for the purposes of providing a home and for intraspecific communication) is an important part of that modified selective environment (Hansell, 2005; Odling-Smee & Turner, 2012).

Given the feedback between genes, culture and constructed environments and considering the fact that social learning is adaptive in humans, in this chapter we aim to explore how human architecture might have evolved to support – or even to galvanize – social learning. More specifically we will zoom in on one general kind of architecture, i.e., religious monumental architecture, and try to shed light on how the specific awe-like emotions that can be elicited by such architecture might have impacted cultural evolution. We will distinguish between two pathways through which awe-evoking religious monumental architecture (RMA) may have enhanced cultural transmission between individuals. First, it may have stimulated cognitive performance underlying learning, leading to – for example – enhanced memory, and in so doing, it supported the reception and retention of cultural variants. Second, it may have provided a social background against which social learning could occur. Specifically, we propose that awe-evoking RMA may have caused individuals to become more prosocially oriented towards others (which increased opportunities for social learning) as well as to have contributed to establishing a learning relationship between religious leaders and commoners.

This chapter consists of two main sections. In the first section we review and discuss evolutionary approaches to architecture. We identify some problems for traditional gene-based approaches to architecture (i.e., architecture as a sexually selected costly signal of genetic quality), and propose an alternative evolutionary approach that also takes ecological and cultural inheritance into account. In the second section we try to shed light on the function of RMA from a cultural evolution perspective, and try to elucidate how the awe-like emotions such architecture can trigger can enhance adaptive social learning in individuals.

Evolutionary approach to architecture

Architecture is somewhat neglected by evolutionary researchers. This is surprising because building is a common and taxonomically broadly distributed behavior in the animal kingdom and it often has dramatic effects on the evolution, ecology and behavior of many species (Hansell, 2005). One influential view on animal architecture is that it is an extended phenotype of the builder, i.e., it counts as an evolvable expression of genes of the builder as much as any other phenotypic trait of the builder, such as fur thickness or body size (Dawkins, 1982).

One of the main functions of animal built structures is intraspecific communication. Commonly these communicative structures are considered to signal genetic quality of the builder to potential mates and/or rivals (e.g., Sergio et al., 2011). One way in which such a structure could be signaling the fitness of the builder, as is often hypothesized, is by its costliness. “Costly signaling” – a formal elaboration of Zahavi’s handicap principle (1975) - predicts that, when there is a conflict of interest between sender and receiver, honest signaling can nonetheless be maintained when the signal is costly and costlier for worse signalers (Grafen, 1990). For example, males of several bowerbird species spend enormous amounts of time and energy on constructing and maintaining decorated bowers, the sole purpose of these being to attract females. Some researchers have suggested that the costliness of a bower functions as a reliable indicator of male genetic quality on the basis of which females make mating decisions (e.g., Wojcieszek et al., 2006).

Some evolutionary archaeologists have attempted to explain human architecture, more specifically (religious) monumental architecture, from a costly signaling perspective. Neiman (1998), for example, proposed that Mayan monumental architecture evolved as a costly signal, reliably signaling the power and wealth (and other proxies of genetic fitness) of its Mayan leaders/builders to commoners (to gain followers) as well as to rivals (to discourage attack). The extreme costs associated with building and maintaining monumental architecture would have paid off in terms of increased power and mating opportunities, and would have deterred rivals and followers from undertaking futile attacks on the Mayan leader(s), which both would have increased reproductive success for the leader(s).

Although the extended phenotype / costly signaling approach is instructive for human architectural constructions, it has some shortcomings. One of the problems is that this approach only takes genetic inheritance into account. If RMA is taken as an instance of costly signaling, the genes of the builder are expressed in architecture and receivers make decisions on the basis of their quality. However, architecture cannot be explained solely in terms of genetic evolution because it also involves ecological and cultural inheritance. Animals that build are *niche-constructing animals*, i.e., they modify or construct their habitat (Hansell, 2005). As a result, a new generation of building organisms does not only inherit genes from the previous generation, but usually also a modified environment. Constructed habitats including architecture are part of that modified environment, giving rise to a second inheritance system: ecological inheritance (Odling-Smee, 2010).

In trying to explain architecture, also ecological inheritance needs to be taken into account because when organisms change their environment they also change the natural selection pressures acting upon them, thus changing the dynamics of the evolutionary process. For example, humans are estimated to have lost their mammalian fur in Africa some 1.6 million years ago as an adaptation to keeping cool (Jablonski, 2010). If genetic inheritance alone had operated, humans would have grown back their fur as a protection against the colder climates of the environments in which they subsequently migrated. Instead, it is likely that humans dampened natural selection for fur by constructing homes and clothes, among other thi ngs.

Cultural inheritance can be viewed as the primary means by which humans engage in the universal process of niche construction. In cultural evolution theory, culture is taken as nongenetic inheritance of culturally acquired information, either directly through social learning between individuals (e.g., imitation, teaching) or through cultural artifacts, such as architecture, both of which can modify the selective environments of organisms, within and between generations (Richerson and Boyd 2005; Odling-Smee, & Laland 2012).

In this chapter we propose a subtle combination between these two modes of cultural transmission (i.e., direct social learning and learning through artefacts). We hypothesize that RMA can be understood as a kind of ecologically inherited, constructed learning environment, which has evolved independently across many large-scale civilizations belonging to different eras and situated in different geographical regions. In our view, the function of RMA is to support, enhance and steer cultural transmission of adaptive information through social learning between individuals. Thus, while Neiman (1998) postulated that RMA evolved as a device to signal genetic information, we propose that it evolved to support transmission of cultural information. Specifically, we hypothesize that, through ecological inheritance, RMA has evolved features such as monumentality to elicit awe-like emotions (e.g., awe, admiration and fascination), which, on their part, positively affect social learning and thus cultural transmission. In the ensuing sections we review evidence from environmental psychology and emotion research that demonstrates that awe-like emotions which are triggered by RMA can affect social learning.

Note that our approach does not look at whether RMA itself contains information which is transmitted, for example, whether it contains information on the genetic quality of the builder, as is the case within the costly signaling framework. We are also aware that in RMA cultural information is often directly displayed to spectators through pictures, paintings, engravings or other visual media. In this chapter we rather focus on RMA as an emotionally charged device or ambient environment, which – through that emotional charging –positively affects social learning and thus cultural transmission of information between individuals.

Religious monumental architecture as galvanizing cultural transmission

The emotion of awe takes in a central place in our account of RMA. While the experience of awe has been an important topic in art theory and philosophical aesthetics (cf., the Sublime), psychologists have shown only little interest in further investigating the particulars of this emotion. One of the few exceptions are Keltner and Haidt (2003), who have developed a "prototypical" account of awe. In their view, two key appraisals are central to the experience of this emotion. On the one hand, Keltner and Haidt (2003) argue that awe entails an intense interest in or fascination for an object, event or phenomenon that is extraordinarily vast compared to the human scale. On the other hand, in order to accommodate the experience of exceptional vastness, a compensatory need arises to adjust mental structures.

Grand natural phenomena or scenes, such as the Grand Canyon or the Niagara Waterfalls, are probably amongst the most widely known elicitors of awe in humans. It is however very likely that cases of RMA that have a comparable splendor and grandeur are also able to spark feelings of awe (Shiota, Keltner & Mossman, 2007). Awe is for example experienced by heritage tourists when they visit cathedrals (Francis, Williams, Annis & Robbins, 2008), and height, which often is characteristic to RMA, has also been found to provoke feelings of awe and respect in human individuals (Schubert, 2005). Monumental constructions (which are often religious) have become part of the modified environment across many large-scale civilizations. Well-known religious monumental edifices are – for example – the Giza Pyramids in Egypt, the gothic Chartres cathedral in France, or Angkor Wat in Cambodia.

Note that the monumental features of religious structures often vastly exceed their direct utility. While spacious cathedral interiors, for example, have direct utility because providing sufficient gathering space (medieval cathedrals also functioned as market places), ceilings of cathedrals are manifold higher than required for gathering. It seems plausible that such monumental features were “added” to religious edifices in order to elicit particular emotions in spectators, and specifically to induce a sense of awe. Our hypothesis is that triggering awe-like emotions had a particular function, namely to enhance transmission of cultural information. Below we will review and discuss three distinct, but interrelated ways in which instances of RMA might have fulfilled that function. First, they enhance the cognitive performance of learning, second, they lead to prosociality, increasing opportunities for social learning, and third, they open up a channel for learning from leaders, thereby increasing learning efficiency.

Cognition

In line with our general hypothesis that instances of awe-provoking RMA are constructed learning environments awe seems to affect cognition in ways that enhance and steer social learning. First, as proposed by Keltner and Haidt (2003) the exceptional vastness that drives awe-experiences can shake up an individual’s mental frameworks, requiring an adaptive need to adjust or update those frameworks. The upshot is that the experience of awe makes the minds of learners open to new informational input that is able to install a new mental “equilibrium”. Note the parallel of our account with the view that one of the main drivers of belief in supernatural agency is cognitive uncertainty or ambiguity (Guthrie, 1993). Our claim is that RMA functions in a somewhat similar way: by provoking awe it exploits cognitive uncertainty and the accompanying compensatory need for accommodation.

Second, the openness which awe can create, entails an openness to particular types of informational input. When in awe people are not so much willing to acquire very concrete cultural information (e.g., what type of clothing to wear) but they seem to be more willing to learn what can broadly be considered as “ideological” content (e.g., religious beliefs, norms, rules, worldviews). This speaks from the fact that awe makes people generally more spiritual (Saroglou, Buxant & Tilquin, 2008; Van Cappellen & Saroglou, 2012) and less interested in material concerns (Keltner & Haidt, 2003: Rudd, Vohs & Aaker, 2012)

Third, the experience of awe cognitively prepares learners for information intake and information retention.

- First, one of the defining features of being awestruck is that it entails a deep degree of fascination for, and interest in the awe-provoking stimulus (Keltner & Haidt, 2003). Vast stimuli can potentially be threatening or harmful, and therefore demand attention. This state of heightened attention, can improve or sharpen the intake of the cultural information that is expressed in association with awe-evoking environments, such as RMA (Shiota, Campos & Keltner, 2003).

- Second, environmental psychology research shows that exposure to environments that evoke a sense of fascination can positively influence cognitive performance (Kaplan & Berman, 2010). Specifically, high-fascinating as opposed to low-fascinating environments can significantly improve working memory (as measured, e.g., by the digit span backwards task, e.g., Berman, Jonides & Kaplan (2008)) and concentration ability (Berto, 2005). Inasmuch as RMA brings spectators into a mode of fascination, these effects can be exploited.
- Third, being in a state of arousal leads to improved memory and retention of the information that is associated with the arousing event or context (McGaugh, 2004). Within the cognitive science of religion, rituals (e.g., initiation rites) have been considered as such highly arousing events (Whitehouse, 2004) during which cultural information is “imprinted”. Quite analogously, we see RMA as a highly arousing environmental context, which facilitates information to become more deeply stored in long term memory.

In our view RMA can bolster cultural transmission because it leads to better attention to and better retention of the cultural information that is expressed or shared in those contexts. There might however be a particular chronological order in these steps. On first encounters with RMA, the awe response is the most intense. At this stage, awe might be exploited to “pull” (new) commoners into the ideology. After a while, however, commoners might get used to the instance of RMA. At that point RMA might no longer lead to full blown awe, but still trigger considerable levels of fascination. Such more “moderate” fascination might be most beneficial to learning, as environments which are fascinating but not too engrossing appear to have the most positive effects on cognitive functioning (e.g., concentration, see: Kaplan & Berman, 2010).

Social interactions

Although openness to new information and sharpened cognitive functioning might lead to an improved disposition to pick up and to remember information, such a disposition is of little value if there is nobody to learn from. In the following two sections we aim to elucidate how awe-like emotions mediate and stimulate formation and consolidation of social learning relationships.

Prosociality

The first way in which experiencing awe can stimulate social learning is through increased prosociality. Specifically, recent research shows that when particular environmental objects or scenes provoke awe, individuals tend to become more prosocially oriented or undertake actions indicative of a prosocial orientation. Shiota and colleagues (2007), for example, report that individuals who had experienced awe felt as belonging to a greater whole, in comparison to individuals having experienced pride. Similarly, Saroglou, Buxant and Tilquin (2008) found that respondents felt a deeper connection and commitment to others and to humanity as a whole after having seen a video-clip of awe-evoking nature than after having watched an amusing video-clip. Individuals who had recalled an awe-eliciting event became more willing to dedicate time (but not money) to others than individuals who had recalled a happy event (Rudd, Vohs & Aaker, 2012).

In addition to increased feelings of oneness with others and with the world, unpublished data collected by one of the authors (YJ) show that awe is a significant and positive predictor of social value orientation. Specifically, when being awestruck individuals become more prosocially oriented and less competitive. Awe also correlates positively with feelings of connectedness with others, and this relationship between connectedness and awe is mediated by feelings of humility. This seems to suggest that some of the social psychology effects of awe are a compensatory strategy for the feelings of smallness and vulnerability that are caused by environmental grandeur.

The foregoing findings thus indicate that one of the typical emotions triggered by RMA – namely awe – stimulates prosocial behavior or, at the very least, provides determinants for human prosociality. Several lines of research in turn demonstrate that prosociality can increase or facilitate opportunities for social learning and can thus bolster cultural transmission and retention of innovations. For example, it has been found that among captive chimpanzees, affiliation promotes the transmission of a social custom, i.e., handclasp grooming (Bonnie & de Waal, 2006). Cultural transmission and retention of a rich set of tool uses in wild orangutans has been shown to depend crucially on tolerant proximity (van Schaik, 2006). In tolerant groups youngsters have the opportunity to learn not only from their mothers but also from other adults in the group. This "oblique transmission" of skills and knowledge appears a necessary condition for the retention of tool behavior in wild orangutans. In humans it has been found that group identification and social value orientation positively affect knowledge sharing amongst group members (Marks, Polak, Mccoy & Galletta, 2008). It is a well-established fact in anthropology that learners preferentially imitate group members whom they identify with on the basis of ethnic markers (Richerson & Boyd, 2005).

The foregoing findings suggest that the establishment and existence of a social fabric and the formation of an identifiable community facilitates the process of sharing and transmitting cultural information among group members, thus enabling cultural information to accumulate. Religious monumental architecture contributed in different ways to such socializing. For example, inasmuch as it provided an enclosed physical space to gather groups of individuals, such buildings probably facilitated social sharing and interaction, hence, bolstering the creation or consolidation of a social fabric. Inasmuch as RMA can also be seen as "materialized ideology" (De Marrais, Castillo & Earle, 1996) or as to symbolize group identity, exposure to such constructions can prime group membership. The view central to our emotion-based account of RMA is that such architecture triggered awe in spectators, increasing feelings of oneness with others, and increasing prosocial orientation. By contributing to building *communitas*, awe-evoking instances of RMA may have stimulated social sharing of information and thus enhanced cultural transmission in RMA-building populations.

Leaders and followers

In addition to increasing closeness between commoners, awe-like emotions evoked by RMA may also function to establish a relationship between a religious leader and commoners, opening up a further channel for social transmission. We differentiate between two possible pathways according to which this learning channel can be opened: one based on dominance and the other one based on prestige (cf., Henrich & Gil-White, 2001). In both pathways the learning relationship is asymmetric: commoners learn from leaders.

A first pathway is that the dominant leader acquires and maintains his dominant position (and hence the asymmetric learning relation) by way of force or threat. The relationship with lower ranked individuals is characterized by aggression, intimidation, violence, fear and compulsion. This appears to be the predominant social ranking system in nonhuman animals, but it still plays a role in humans as well (Henrich & Gil-White, 2001). Despite some controversy, it is generally accepted that dominance correlates with fitness, due to privileged access of dominant individuals to space, food, and mates (for males) (Ellis, 1995). The stability of dominance is often reinforced with “reminders”: intimidation by the dominant individual and submissive behaviors from the low(er) ranked to the high ranked individual (e.g., grooming, submissive displays). RMA might be such a reminder, one of the dominant religious leader’s tools to induce submission in commoners. Monumentally high structures may for example induce submissiveness and anxiety in perceivers, or alternatively, the use of elements such as pointy spires in gothic cathedral architecture might induce fear by mimicking predator teeth (Larson et al., 2009).

Note that learning that occurs through this pathway is not social learning in the strictest sense. In cultural evolution theories social learning implies that social learners ‘freely choose’ which cultural variants to adopt (on the basis of content or context biases) (Henrich & McElreath, 2003). Learning, within a threat-based relationship (as described above) is rather imposed copying. The dominant leader enforces rules, norms, or even beliefs onto lower ranked individuals. Although neglected within current cultural evolution theory, it seems that this learning pathway is relatively common. For example, in Africa colonialism often went hand in hand with cultural imperialism and oppression, which nonetheless led to sustained adoption of some of the colonizer’s cultural variants, even long after independence (Reybrouck, 2010).

A second pathway to establishing a learning relationship is that a prestigious leader acquires and maintains high status not by force but by having attained excellence in a valued domain of activity, without making any credible claims to superior force. Henrich and Gil-White (2001) argue that the evolutionary and psychological processes involved in prestige hierarchy systems are fundamentally different from the ones in dominance hierarchy systems. Prestige processes emerge, they assert, from human evolved social learning psychology. Based on the fact that social learning is adaptive, selection favored the evolution of psychological biases that increase social learning efficiencies. Prestige bias, defined as the capacity to identify and preferentially copy models who are likely to possess better-than-average information, is one such a bias. Thus the most knowledgeable/skillful models will end up with the biggest and most lavish “clientele” (i.e., copiers), with the size and the lavishness of a given model’s clientele (the prestige) providing a reliable proxy for that person’s information quality. In order to gain greater access and cooperation, the clientele provides all kinds of fitness-enhancing benefits (i.e., "deference") to the prestigious individuals. Prestigious leaders are therefore motivated to show off the amount of deference they get and to elicit ever more admiration.

We propose that prestigious religious leaders use RMA to achieve exactly that goal. Henrich and Gil-White (2001) note that prestige – as commonly understood - has nothing to do with being feared or with being begrudged, but that it rather involves emotions such as, respect, devotion, love and… awe. Thus, insofar as RMA evokes awe, it may do so for regulating and enhancing beneficial interactions between prestigious religious leaders and their clientele of followers. In contrast to the dominance pathway, in the prestige system awe will lean more towards admiration and devotion and much less to fear. Note however that both dominance and prestige systems can operate (simultaneously or subsequently) in human social ranking systems (Henrich & Gil-White 2001). For example, while a leader may first have acquired status by excellence and prestige, when followers do no longer show sufficient deference, the leader might become compelled to make recourse to fear and threat to maintain his social position.

Conclusion

In this chapter we have explored whether religious architecture is often monumental because monumentality can elicit awe-like emotions, which, on their part, stimulate and steer cultural transmission of adaptive information and (religious) behavior. Our exploration, based on findings from emotion research and environmental psychology, tentatively suggests that awe-evoking RMA may indeed fulfill this role. In our view, RMA galvanized cultural evolution by sharpening cognitive performance underlying learning, by steering the adoption of particular cultural contents, and by increasing opportunities for and efficiency of social learning interactions. The image we have sketched of RMA fits well with the theoretical framework of (cultural) niche construction (Odling-Smee & Laland, 2012), which predicts that the environment an organism constructs, often alters selection pressures on cultural and/or genetic inheritance.

References

Berman, M.G., Jonides, J., & Kaplan, S. (2008). The cognitive benefits of interacting with nature. *Psychological Science*, 19, 1207–1212.

Berto, R. (2005). Exposure to restorative environments helps restore attentional capacity. *Journal of Environmental Psychology*, 25, 249-259.

Bonnie, K.E., & de Waal, F.B.M. (2006). Affiliation promotes the transmission of a social custom: handclasp grooming among captive chimpanzees. *Primates*, 47, 27–34.

Boyd, R., Richerson, P.J., & Henrich, J. (2011). The cultural niche: Why social learning is essential for human adaptation. *PNAS*, 108, 10918–10925.

Boyd, R., & Richerson, P.J. (2005). The Origin and Evolution of Cultures, Oxford University Press, New York

Dawkins, R. (1982). *The extended phenotype*. Freeman, New York

De Marrais, E., Castillo, L.J., & Earle, T. (1996). Ideology, materi alization, and power strategies. *Current Anthropology*, 37, 15–31.

Ellis, L. (1995). Dominance and reproductive success among nonhuman animals: A cross-species comparison. Ethology and Sociobiology, 16, 257–333.

Francis, L.J., Williams, E., Annis, J., & Robbins, M. (2008). Understanding Cathedral visitors: psychological type and individual differences in experience and appreciation. *Tourism Analysis*, 13, 71–80.

Grafen, A. (1990). Biological signals as handicaps. *Journal of Theoretical Biology*, 144,246-517.

Guthrie, S. (1993). *Faces in the Clouds: A New Theory of Religion*. Oxford: Oxford University Press.

Hansell, M.H. (2005). Animal Architecture. Oxford: Oxford University Press.

Henrich, J., & Gil-White, F. (2001). The evolution of prestige: Freely conferred status as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior*, 22, 165-96.

Henrich, J., & McElreath, R. (2003). The evolution of cultural evolution. *Evolutionary Anthropology*, 12,123-35.

Jablonski, N.G. (2010). The Naked Truth: Why Humans Have No Fur. *Scientific American, 302*, 28-35.

Kaplan, S., & Berman, M.G. (2010). Directed attention as a common resource for executive functioning and self-regulation. *Perspectives on Psychological Science*, 5, 43–57.

Keltner, D., & Haidt, J. (2003). Approaching awe, a moral, spiritual, and aesthetic emotion. *Cognition and Emotion*, 17, 297–314.

Larson, C.L., Aronoff, J., Sarinopoulos, I.C., & Zhu, D.C. (2009). Recognizing threat: Simple geometric shapes activate neural circuitry underlying threat detection. *Journal of Cognitive Neuroscience*, 21, 1523–1535.

Marks, P., Polak, P., Mccoy, S., & Galletta, D. (2008). Sharing knowledge. *Communications of the ACM*, 51, 60–65.

McGaugh, J.L. (2004). The amygdala modulates the consolidation of memories of emotionally arousing experiences. *Annual Review of Neuroscience*, 27, 1–28.

Neiman, F. (1998). Conspicuous consumption as wasteful advertising: A Darwinian perspective on spatial patterns in Classic Maya terminal monument dates. In C. M. Barton, & G. A. Clark (Eds.), *Rediscovering Darwin: Evolutionary theory in archaeological explanation* (pp. 267–290). Arlington, VA: American Anthropological Association.

Odling-Smee, J. (2010). Niche inheritance. In: Pigliucci M, Müller GB (eds) *Evolution: the extended synthesis*. MIT Press, Cambridge, MA, pp. 175–207.

Odling-Smee, J., & Laland, K.N. (2012) Ecological Inheritance and Cultural Inheritance: What Are They and How Do They Differ? *Biological Theory* 6, 220-230.

Odling-Smee, J., & Turner, S.J. (2012). Niche Construction Theory and Human Architecture. *Biological Theory*, 6, 283-289.

Reybrouck, D. (2010). Congo. Een geschiedenis [Congo. A history]. Amsterdam: de Bezige Bij.

Rudd, M., Vohs, K. D., & Aaker, J. (2012). Awe expands people's perception of time, alters decision making, and enhances well-being. *Psychological Science*, 23, 1130-1136.

Saroglou, V., Buxant, C., & Tilquin, J. (2008). Positive emotions as leading to religion and spirituality. *The Journal of Positive Psychology*, 3, 165–173.

Schubert, T. (2005). Your highness: Vertical positions as perceptual symbols of power. *Journal of Personality and Social Psychology*, 89, 1–21.

Sergio, F., Blas, J., Blanco, G., Tanferna, A., López, L., Lemus, J.A., & Hiraldo, F. (2011). Raptor nest decorations are a reliable threat against conspecifics. *Science, 331*, 327-330.

Shiota, M.N., Campos, B., & Keltner, D. (2003). The faces of positive emotion: Prototype displays of awe, amusement, and pride. *Annals of the New York Academy of Sciences*, 1000, 296-299.

Shiota, M., Keltner, D., & Mossman, A. (2007). The nature of awe: Elicitors, appraisals, and effects on self-concept. *Cognition and Emotion*, 21, 944–963.

Van Cappellen, P., & Saroglou, V. (2012). Awe activates religious and spiritual feelings and behavioral intentions. *Psychology of Religion and Spirituality, 4,* 223-236.

van Schaik, C. (2006). Why are some animals so smart? *Scientific American* 294, 64–71.

Whitehouse, H. (2004). *Modes of religiosity: A cognitive theory of religious transmission*. Lanham, MD: Rowman & Littlefield.

Wojcieszek JM, Nicholls JA, Marshall NJ, Goldizen AW. 2006. The stealing of bower decorations among male satin bowerbirds (*Ptilonorhynchus violaceus*): why are some decorations more popular than others? *Emu*, 106, 175–180.

Zahavi, A. (1975) *Mate selection - a selection for a handicap*. Journal of Theoretical Biology. 53: 205-214.

Chapter 6: An Exploration Of The Functions Of Religious Monumental Architecture From A Darwinian Perspective

Introduction

Monumental architecture has been independently expressed across many large-scale civilizations belonging to different eras and situated in different geographical regions. Well-known monumental structures are—for example—the Giza Pyramids in Egypt, Angkor Wat in Cambodia or the Teotihuacan Pyramids in Mexico (Trigger, 1990). It is commonly assumed that the defining feature of such monumental constructions is their large scale, which vastly exceeds the scale of the everyday buildings and built structures of the epoch in which they were built. Very probably, experiencing a particular edifice as monumental depends on the particular time frame or the culture in which one lives, as well as on one's previous exposure to built monumental structures. For example, whereas for a 21st century urbanite, accustomed to massive modern skyscraper buildings, Neolithic ashmounds might not look particularly spectacular, these structures probably felt as considerably more impressive for Neolithic people, for whom they were among the biggest built structures of their era (Johansen, 2004).

Throughout architectural history different types of monumental architecture have been constructed. In early civilizations, fortifications, palaces, temples, and tombs were among the most com- mon types, whereas in classical Rome and Greece, public build- ings such as arenas, theaters, or public baths also often exhibited monumental aspects (Trigger, 1993, p. 75). In this article, we will concentrate on monumental architecture that was built to fulfill particular functions related to religious doctrines, that is, religious monumental architecture (RMA). Although the possible roles of monumental architecture for religions have already been briefly hinted at in evolutionary accounts of religions and religious behavior (e.g., Gervais & Henrich, 2009; Atran & Henrich, 2010), in this article we aim to give an in-depth and tentative analysis of the potential function(s) of this type of architecture for religious doc- trines.

The theoretical backdrop of our analysis is the view that religions are complex “devices” that help(ed) creating, regulating and enacting (large-scale) community living (e.g., Wilson, 2002; Graham & Haidt, 2010). In agreement with Graham and Haidt (2010) paper we see religion as “... a complex system with many social functions, one of which is to bind people together into cooperative communities organized around deities” (p. 140). This perspective on religion has received much attention in recent evolutionary approaches to religion and has bolstered research into the relation between religiousness and cooperative, prosocial behavior (e.g., Shariff & Norenzayan, 2007). The question as to whether religions’ social function came about as a result of selection pressures at the level of the individual, the group, or both (cf., Wilson, 2002) is still unsettled. Rather than choosing sides of either one of these positions, we aim to shed light on the mechanism(s) through which RMA supported religions’ social function.

Within the field of archaeology, monumental architecture is some-times interpreted as a costly signal that evolved to deter rival (religious) elites (Neiman, 1998). In this chapter, we will argue that in order to fully understand the cultural and temporal pervasiveness of RMA, this costly signaling account needs to be complemented with insights from sensory exploitation theory (Ryan, 1998). Sensory exploitation is a concept from biological signaling theory that grasps how in animal communication particular sensory sensitivities can be exapted. In this chapter, we will argue that not only the costliness underlying RMA supports the social function(s) of religion, but also the fact that such architecture seems to tap into an adaptive “sensitivity for big- ness.” In so doing, RMA exploits a particular emotional response (i.e., awe), which—we hope to demonstrate—supports the process of religious community building.

This article is organized as follows. In the first section, we offer a discussion of Darwinian approaches to monumental architecture. We complement and extend the view that such edifices are costly signals, and claim that sensory exploitation theory has additional explanatory value to explain the occurrence of RMA. We conjecture that, although being a costly signal, RMA also plays on the adaptive tendency to associate size cues with dominance/power, both of which may trigger awe in spectators. The two following sections aim to demonstrate how experiencing awe supports the social function of religions. Specifically, in the second section it is argued that awe-provoking instances of RMA contribute to vertical stratification within religious communities, to bonding between (religious) community members and to monitoring social life. The third part discusses the relationship between RMA and religious beliefs. Such edifices are specifically deemed to be commitment signals, whose specific emotional charging creates in religious followers an openness to religious/supernatural beliefs. The fourth section suggests that RMA’s social function can only be fully grasped if seen as being intimately intertwined with religious ritual behavior and activities.

Darwinian Approaches to (Religious) Monumental Architecture

A number of (archeological) researchers have attempted to shed light on the origin and function(s) of monumental architecture from a Darwinian perspective. In the following sections, we con- sider the specific evolutionary model that is commonly invoked by these researchers, that is, costly signaling theory, and complement it with sensory exploitation theory. We further discuss one particular sensitivity we think is exploited by RMA, and dwell on a typical emotional response that can derive from this exploitation process and from observing the costliness underlying cases of RMA, namely awe. For our discussion of awe we mainly rely on Keltner and Haidt's prototypical account of awe (Keltner & Haidt, 2003).

Monumental Architecture as a Costly Signal

The archeological record shows that there is a correlation be- tween the emergence of monumental architecture and the rise of stratified communities (e.g., Trigger, 1990; Kolb, 1994; De Marrais, Castillo, & Earle, 1996). Based on this, some authors presume that building monumental architecture actively contributed to vertical social stratification. But by which mechanism could this have happened? One view which has received considerable attention in the literature on monumental architecture is that monumentality is a nonambiguous and reliable signal of power. Trigger (1990), for example, argues that building monumental architecture required massive amounts of energy, and only those who actually had power and controlled it could have been capable of recruiting and managing the energy and labor necessary for building such edifices. Monumental buildings thus ". . . symbolize the ability of those for whom they were made to control . . . energy to an unusual degree" (Trigger, 1990, p. 125). By participating in constructing such power symbols, commoners acknowledged their lower ranking with regard to the leading elites, which further underlined their social inferiority. As embodying vast amounts of labor and energy, and the elites' ability to control these, monumental architecture became one of the instruments for achieving social organization/ stratification.

Although Neiman (1998) also recognizes the social organizational role of monumental architecture, his main interest lies in elucidating, from a Darwinian perspective, how wasting energy on nonutilitarian monumental architecture could have conveyed an adaptive benefit to the elite builders. There are different indications that such buildings actually did have little pragmatic, that is, nonsignaling use. For example, monumental structures could oftentimes not be accessed, or only by a small religious elite. When such type of architecture could be entered by the public (cf., churches or cathedrals), the roofing of the interior space often surpassed the height that was strictly necessary for the events and activities taking place there (e.g., religious services, marketplace). The fact that, at times, this increased the risk of collapse suggests that the shape of the building surpassed its specific utilitarian/ pragmatic requirements. Also the use of visual illusions in religious monumental architecture, which further augments the apparent grandeur of the structure, illustrates that, over and above possible pragmatic functions, such architecture was also built to impress its viewers (for a further discussion of this issue, see below, "Religious Monumental Architecture Exploits Awe").

By relating the occurrence of monumental architecture to Zahavi's handicap principle (Zahavi, 1975), Neiman (1998) attempts to theoretically extend Trigger's (1990) account. Specifically, building on a case study of classic Mayan monumental architecture, he contends that such "wasteful" constructions illustrate costly signaling. Such edifices are analogous to nonhuman animal threat displays, like costly nest decorations of black kites (Sergio et al., 2011). They reliably signal that the elites who have built them had an energy surplus over competing elites and signaled to the latter that engaging in competition would be futile. To non- elites they provided an opportunity to accurately assess the elites' qualities as potential leaders (Aranyosi, 1999). Monumental architecture can thus be considered as '. . . a form of "smart advertising," wherein the signaler accrues the benefits of increased access to labor and resources as a result of paying the cost of construction, and nonsignalers can benefit from associating with more capable elites' (Aranyosi, 1999, p. 357). Because monumental architecture thus signaled superior competitive ability, the elites who built these structures had privileged access to resources and mates, which ultimately increased their reproductive fitness.

In both Trigger (1990) and Neiman's (1998) account, it is mainly by wasting energy through labor and resources that monumental architecture plays it social organizational role. We suspect, however, that a mere focus on wastefulness cannot fully capture the characteristics of RMA. The reason is although a costly signaling perspective focuses on the effort/energy that has gone into creating the architectural form, it remains silent on the question of how these structures' particular aesthetic appearance might also have contributed to some of the proposed functions of RMA, such as social organization/stratification.

In our framework, we bring together two theoretical perspectives to explain the functions of RMA. We agree with Neiman (1998) that many instances of RMA are costly signals, illustrating wastefulness of—among other things—time, material, or labor. However, claiming that RMA merely embodies wastefulness greatly underconstrains the precise form of these edifices. The history of architecture shows us that during different epochs and among different cultures wasteful advertising through monumentality mainly occurred by erecting structures whose most constant and distinctive feature is their very large size, most often expressed through height (cf., towers, pyramids, ziggurats). This historically constant feature is not addressed by signaling accounts of monumental architecture.

There is little doubt that concentrating the waste of energy and material into one massive structure that stands out from the environment allows observers to fairly easily estimate the effort that has gone into building the structure. We are, however, convinced that something more than signal efficiency is operating here (Endler, 1992). In our dual account of RMA, Neiman's costly signaling account is complemented with another theoretical perspective on signal evolution, namely sensory exploitation theory. In so doing, we hope to further address the question of why exactly size, and specifically, height, have become attractors for wasteful monumental building activities. In the following sections, we explain the basic principles of sensory exploitation theory and try to demonstrate that the primary sensorial sensitivity being exploited in RMA is an adaptive "sensitivity to bigness."

Religious Monumental Architecture Involves Sensory Exploitation

The mechanism of sensory exploitation.

In a costly signaling system, receivers' responses to senders' signals are determined by the extent to which these signals indicate underlying (genetic) quality of the sender (Zahavi, 1975). Although being an influential perspective, in animal communication research costly signaling is only one of the many models which biologists use to explain how signals evolve. Another model that has received much attention is sensory exploitation (SE; e.g., Ryan, 1998; Arnqvist, 2006). Central to SE is that senders evolve display traits to exploit preexisting sensitivities of receivers,[12] or sensitivities that are under strong selective pressure in another context than the SE system. These traits may often be costly, but that does not necessarily mean that they reliably correlate with quality, which is a requirement to regard the trait as a costly signal. In recent years, theoretical (e.g., Fuller, Houle, & Travis, 2005) and empirical evidence (e.g., Rodriguez &

[12] Usually the term "sensory exploitation" is interpreted quite broadly, referring not only to the exploitation of sensory sensitivities, but also to the exploitation of receivers' emotional and cognitive sensitivities. Moreover, these sensitivities do not need to be innate, but can be learned as well, given that they are maintained by strong functionality outside the signaling context. Therefore, sometimes the more inclusive term "receiver psychology" is used.

Snedden, 2004) for the role of SE in sexual selection has been steadily accumulating, establishing it as a valuable alternative to traditional indirect benefit models, such as costly signaling.

Several empirical studies lend support to the plausibility of the SE mechanism as an alternative account of signal evolution (for a review, see Fuller et al., 2005; Arnqvist, 2006). For example, Rodd, Hughes, Grether, and Baril (2002) suggest that male guppy color patterns are food mimics. Specifically, they found that, among populations, variation in female mating preferences for males with orange spots can be explained by the attraction to orange food objects. Given the fact that these animals frequently eat orange food items, selection for easy detection of orange food items might have resulted in selection for preferences for orange males.

We admit that demonstrating a correlation between attraction to orange food and orange males, by itself, does not tell us anything about the direction of causation. It may be that the "orangeness" of males is actually an adaptive indicator of male quality (because, for instance, producing the color requires ingesting carotenoids), and that the preference for orange food is merely a by-product of mate choice. It may also be that the preference for orange food and orange males evolved independently in these guppies (Fuller et al., 2005). A final possibility is that costly signaling and SE operate simultaneously and complement each other, and thus, each ex- plains a particular aspect of the evolved display. In the case of the guppies example, it may be that, initially, females are attracted to orange males because they mimic food. Because this orangeness is also hard to produce for males, females can—secondarily—also be selecting for male quality (Arnqvist, 2006).

This last interpretation is a "weaker" version of SE, one that is not mutually exclusive with costly signaling and that may even complement it. This account is commonly considered to explain specific aspects of costly signal evolution, for example, why a costly signal takes on a specific wasteful form rather than another one. This weaker version of SE is also called "sensory drive" and often focuses on signal efficiency (Endler, 1992). It needs mention, however, that a clear distinction between sensory drive and SE is unwarranted and usually these theoretical variants are lumped together. The argument put forward in this chapter is mainly based on this weaker version of SE. In particular, we propose that in addition to costly signaling, SE has explanatory potential for RMA and can uncover why in RMA costliness is perennially embodied in high structures.

Although both SE and costly signaling are usually applied to explain patterns in sexual selection, they can also describe the interactions between senders and receivers of any signaling sys- tem, even a cultural one. Whereas in sexual selection, SE drives the evolution of male display signals (e.g., ornaments, behaviors, sound production) in the signaling system, we propose SE drives the evolution of particular features about RMA (i.e., increased size and height of built structures) to reinforce religions' social function. Sensory exploitation operates because receivers have preexisting sensory, cognitive, or emotional sensitivities for visual, aural, or other perceptual stimuli/features. In our signaling system RMA is supposed to exploit what we coin a "sensitivity for bigness."

Religious Monumental Architecture exploits an adaptive sensitivity for bigness.

The primary sensory sensitivity that seems to be exploited by instances of RMA is the tendency to consider large-sized objects or agents as powerful or dominant. This sensitivity seems to be widespread in the animal kingdom. With regard to humans it has been suggested that it originates from parent–child interactions, wherein the correlation between the parent's size and its influence over the child becomes a benchmark for estimates about social power later on in life (Schwartz, Tesser, & Powell, 1982). Others, however, consider such a "sensitivity for bigness" to be a deeply homologous trait, which might explain why it is shared among different animal species. Judge and Cable (2004), for example, note that in the animal kingdom height and size are employed to assess the power and strength of other animals, thus acting as a direct cue on the basis of which fight-or-flight decisions are made. According to this view, a sensorial sensitivity to bigness is basically adaptive perception. Within groups of (social) animals, this sensitivity for bigness seems to be exploited during dominance displays, in an effort to establish or further consolidate social hierarchies (De Waal, 1982). For example, during dominance displays of nonhuman primates dominant individuals try to make themselves appear taller than they actually are (e.g., by extending arms and legs) and also exhibit traits (e.g., pilo-erection) which increase their perceived size (De Waal, 1982). In captivity, primates have even been reported to intensify the power of their display by making high structures with some of the objects available in their enclosures.

The association of size cues with power is also apparent from human behavior. For example, bank directors' offices are often located in the uppermost parts of office buildings, whereas after sporting contests the winner is invited to take the top spot on the podium. Empirical research shows that individuals who take on postural positions that augment their perceived size feel more powerful than their "constricted" counterparts (Huang, Galinsky, Guenfueld, & Guillory, 2011) and are commonly considered as more socially dominant by viewers (Marsh, Henry, Schechter, & Blair, 2009; see also Tiedens & Fragale, 2003). Higher social power/ranking is also attributed to human figures who are placed on an elevation, as opposed to figures in a nonelevation position (Schwartz et al., 1982). When faces are presented in a raised position they are evaluated as being more dominant than their "lowered" equivalents (Mignault & Chaudhuri, 2003). Recent re-search suggests that, in humans, this sensitivity for bigness is already present from a very early age. In specific, Thomsen, Frankenhuis, Ingold–Smith, and Carey (2011) report that, as of 10 months old, infants use relative size as a cue for predicting dominance in a conflict of goals.

Of relevance for our argument about RMA is that this sensitivity for bigness does not only become activated by a social agent's body size or by its specific bodily posture (e.g., grandstanding). Recent research demonstrates that already very simple height, verticality, and size cues create impressions of power. Although the effects of such cues are mainly studied from the perspective of embodied cognition research, they are consistent with the evolutionary perspective taken in this chapter. For example, Schubert (2005) showed (among others) that respondents are faster at identifying powerful groups when these groups were represented on top of a computer screen than at the bottom, supporting the view that the concept of power is visually represented as a vertical difference (see also: Fiske, 1992; Haidt & Algoe, 2004). In an organization chart, when the vertical line that connects the leader to the employees is made longer, then the leader is judged as being more powerful (Giessner & Schubert, 2007). Schubert, Waldzus, and Giessner (2009) found that subjects were faster and more accurate in indicating whether a concept described a powerful group (e.g., "professor") when this concept was written in large as opposed to small fonts, which is consistent with the view that size cues correlate positively with perceptions of power. Similar results speak from the fact that dominant individuals have a visual preference for the vertical dimension in space (Moeller, Robinson, & Zabelina, 2008) and that activating concepts referring to powerful groups/individuals (e.g., "president") drives attention to higher spatial positions (Zanolie et al., 2012).

We hypothesize that inasmuch as size, and especially height, is characteristic to RMA, such edifices can be interpreted as cultural signals that exploit in spectators the sensitivity for bigness, that is, the tendency to see and feel power/dominance in objects/features that are big, or at least suggest bigness. This particular claim receives further support from the finding that power and dominance are also associated with ecologically relevant stimuli (i.e., mountainous topographies; Gagnon, Brunyé, Robin, Mahoney, & Taylor, 2011), and not only with the aforementioned simple height, verticality, or size cues. Thus, in addition to the fact that in RMA power is evident from the fact that massive amounts of energy and labor were necessary to erect these structures (cf., Trigger, 1990; Neiman, 1998), the SE perspective extends that view by suggesting that also particular formal attributes of these buildings (especially height) lead to subjective impressions of power.[13]

Religious Monumental Architecture galvanizes cultural evolution.

According to the frame- work outlined so far, instances of RMA not only signal wastefulness (cf., Neiman, 1998), but they also tap into an adaptive sensitivity for bigness. It is worth noting that the two components central to our dual account of RMA (i.e., costliness, bigness) are not exclusive to human built accomplishments, but are sometimes even characteristic to animal constructions. Consider for example, the Vogelkop bowerbird species, which builds bowers that are many times higher than their makers. Such structures too seem to be characterized by both costliness (in precision and construction cost) and monumentality (in size). This conspicuous similarity between (aspects of) certain human and animal constructions illustrates how cross-species comparisons can shed light on the possible ultimate functions of human building behavior, suggesting that also the aesthetics of human architecture is constrained by evolutionary factors (see, e.g., Hersey, 1999).

In the bowerbird example, female bowerbirds use the male bower as quality indicators of its builder. Analogously, in Neiman's account (Neiman, 1998), building monumentally is assumed to convey a fitness advantage to their Mayan builders because the fact that they were able to expend valuable amounts of energy and resources on such inherently useless structures reliably illustrated their genetic fitness. In our dual account, however, the function of RMA should not necessarily be restricted to a sexual selection framework (cf., Miller, 2000). Rather than solely serving genetic transmission, RMA can also be a vehicle for cultural transmission. For example, according to dual inheritance theory (DIT; Richerson & Boyd, 2005) culture—being understood as "knowledge stored in brains" —is adaptive, and the evolution and transmission of cultural variants is driven and guided by social learning, imitation, and teaching. Of particular interest is that cultural learners employ a number of fast and frugal heuristics to identify good learning models that allow them maximize the success of social learning. Learners are, for example, biased to learn from and imitate models (e.g., individuals or groups) that send out signals that are indicative of

---

[13] Along similar lines, clothing and garments that artificially increase an individual's height (cf., thick boots, high heels, tall hats, miters) can be understood as culturally evolved objects that exploit the sensitivity to bigness. Like RMA, they are perhaps one of the possible ways in which people use designed elements or artifacts to appear powerful and dominant.

cultural success, such as prestige (Henrich & Gil– White, 2001). Inasmuch as massive religious edifices signal prestige, such structures can galvanize the transmission of the particular cultural variants adhered to by the cultural models that have been involved in building them. One of the central tenets of DIT is that cultural and genetic evolution do not always operate in unison. Dual inheritance allows to view the prestige which RMA enjoys not only as an indicator of good genes, but also as an indicator of good "cultural variants," thus being one of religions' devices to promote and facilitate their own cultural dissemination.

Religious Monumental Architecture exploits awe.

Having sketched the main lines of our dual account of RMA, in the next sections, we will turn to another aspect which has received little attention in accounts of monumental architecture, namely, the emotions that are experienced when encountering such massive structures. In Neiman's costly signaling account (Neiman, 1998), the emotional impact of RMA remains largely implicit. Our aim is to open this black box and to bring the "hot," that is, the emotional impact of RMA, to the foreground. Specifically, our account attributes a central role to the emotion of awe, and attempts to explain how its experience interlocks with RMA, and the associated religious doctrine's possible functions. In the ensuing sections, we first give a brief overview of the central characteristics of awe, after which we discuss which characteristics of RMA might possibly trigger this particular emotion.

Central characteristics of awe – "vastness" and "need for accommodation".

Religious monumental architecture can trigger a wide range of emotions in human individuals, among others admiration, beauty, delight, goose bumps, aesthetic chills, fear, dizziness, romance, or hope. One of the core assumptions of the argument put forward in this chapter is that a common and frequent emotional response on perceiving instances of RMA is—and always has been— awe. Although grand natural scenes are perhaps among the most widely known elicitors of this emotion (cf., the Grand Canyon), it is very likely that cases of religious monumental architecture that have a comparable splendor and grandeur are also able to spark feelings of awe (Shiota, Keltner, & Mossman, 2007). Awe is, for example, experienced by heritage tourists upon visiting cathedrals (Francis, Williams, Annis, & Robbins, 2008), and height, which often is characteristic to RMA, has also been found to provoke feelings of awe and respect in human individuals (Schubert, 2005). As will be argued further on, triggering this particular emotional response supports the community function of religions.

The emotion of awe has received a fair bit of attention in the religious, philosophical, and sociological literature, but it is only since the last decade that it has become studied from a psycho- logical perspective, albeit still to a limited extent (e.g., Keltner & Haidt, 2003; Shiota et al., 2007; Armstrong & Detweiler–Bedell, 2008). One of the most in-depth psychological discussions of this emotion has perhaps been provided by Dacher Keltner and Jonathan Haidt (Keltner & Haidt, 2003). In their "prototypical" approach to awe, Keltner and Haidt consider awe to primordially be a social emotion, which can be traced back to the submissive feelings which (low-ranked) individuals experience in the face of powerful individuals or leaders. The adaptive function of this emotion, they maintain, is to affirm and consolidate prevailing social hierarchies. A crucial point, according to Keltner and Haidt (2003), is that awe is not only experienced in response to powerful or dominant social agents, but ". . . generalizes to other stimuli . . . to the extent that these new stimuli have attributes associated with power" (Keltner & Haidt, 2003, 306–307).

Based on a reading of the relevant literature on awe, Keltner and Haidt (2003) contend that two primary appraisals are at the heart of prototypical awe experiences. First, awe can arise when (social or nonsocial) stimuli are encountered that are powerful or "vast" with regard to a particular frame of reference (Keltner & Haidt, 2003; see also Shiota et al., 2007). According to Keltner and Haidt (2003) "vastness" should not necessarily be restricted to physical size, as applies for example to the majestic Pyramid of the Sun at Teotihuacan (Mexico). Awe-inspiring stimuli might—among other qualities—also be vast in time, space, degree of elaboration, or ability. On this account, recognizing that gargantuan efforts have gone into constructing a religious monumental structure might also color one's experience of the edifice with awe.

If only appraisals of vastness were to occur in response to a particular stimulus, people would probably be more likely to feel—say—reverence or submission, rather than awe. According to Keltner and Haidt (2003) full-blown awe only occurs when this vastness is of an overwhelmingly high intensity. Put differently, by its "vastness," the awe-evoking stimulus does not only coopt the human sensitivity for dominance signals, but it also becomes a superstimulus by exceptionally exaggerating that vastness (Tinbergen, 1951). Although such exceptional vastness can create a sense of physical insignificance in spectators, Keltner and Haidt (2003) contend that the second important dimension of awe relates to how individuals cognitively appraise those feelings of insignificance. In specific, the experience of exceptional vastness deeply challenges or "shakes" an individual's cognitive conceptions, involving an inability to assimilate the awe-provoking experience into current mental structures. This is supposed to trigger a compensatory need to "accommodate" the awe-filled experience, involving an adjustment of existing mental schemes (Keltner & Haidt, 2003). Notice that such awe-provoking, (cognitively) overwhelming vastness often seems to be an intrinsic characteristic of instances of RMA. For example, the Notre Dame Cathedral in Paris very probably triggered awe in the medieval peasant population because its splendor and massive scale was unlike any built structure they had ever seen. It largely surpassed these individuals' mental conceptions of possible human creative accomplishments.

Note that underlying the argument that RMA is/was a common trigger of awe is the assumption that RMA has had similar emotional effects across different cultures and epochs. But is there any evidence for this? Already two decades ago, Ekman (1992) speculated that awe should be considered a basic emotion, but he also noted that empirical support for this speculation was lacking. Likewise, Haidt and Keltner (2002) anticipate that awe is experienced among most cultures, although there might be between- cultural variation in the importance attached to the emotion. Although systematic research is lacking, there are some indications for the cross-cultural prevalence of awe. For example, in the Natyashastra, an ancient Indian treatise on the performing arts, awe/wonder ("Vismaya") is an essential part of the repertoire of nine basic emotional responses. Research by Haidt and Keltner (1999), furthermore, shows that both American and Indian respondents employ awe to label particular emotional facial expressions (Haidt & Keltner, 1999), whereas these two cultural groups are also able to correctly identify wonder/awe in the dynamic (facial and bodily) expressions in classic Hindu dance performances (Hejmadi, Davidson, & Rozin, 2000). From a cross-species perspective, so-called "waterfall-displays" by chimpanzees are some- times associated with awe. Although such displays involve the primates to dance near the waterfalls that emerge after heavy rainfalls, they have also been found to contemplate this natural event for many minutes, as if standing in wonder and awe about it (Goodall, 1986). Thus, although more empirical research is required to settle the issue as to whether awe occurs cross-culturally and cross-temporally, these studies and observations at least tentatively suggest that it is likely to be the case.

Triggers of Awe in Religious Monumental Architecture.

But what exactly is it about RMA that can trigger awe? In accordance with Keltner and Haidt's (2003) prototypical approach to awe, the vastness inherent to RMA can be considered as the primary cause of awe. But what does this "vastness" exactly amount to? First of all, vastness can—of course—refer to the sheer physical size of the monumental structure. However, the "raw" or absolute scale of RMA is probably not the only physical source of awe. Consider the fact that in human mate choice, large breasts and buttocks can provoke awe or awe- related states in males, whereas large upper body muscles can trigger awe in females. These observations suggest that awe is based on implicit contrasts to what is normal, rather than on absolute scale. Monumental (religious) structures, such as cathedrals or pyramids, are massive and awe-evoking, even by today's standards (pyramids, cathedrals; see Figure 1 for examples of RMA). However, despite the fact that many monumental built structures of small-scale societies are considerably smaller absolutely, they were still much larger than any surrounding structures, and could therefore well have been a source of awe during their epoch. Our argument thus not only applies to the "traditional" examples of RMA, like pyramids or cathedrals, but extends to monumental structures such as ashmounds, barrows, longhouses, or stone circles (e.g., Stonehenge).

Figure 1. An example of religious monumental architecture. The Pyramid of the Moon at Teotihuacan, Mexico.

As outlined in our characterization of awe (see "Religious Monumental Architecture Exploits Awe"), certain immaterial characteristics can also be considered as "vast," such as the "big" personality of charismatic leaders (cf., Martin Luther King), or extraordinary physical accomplishments (e.g., finishing an ultra-marathon). In an analogous way, the (effortful) processes involved in, or necessary for constructing monumental religious buildings (e.g., the vast amount of work) can also be a source of "vastness" (besides direct physical appearance). Building monumentally al- most per definition requires huge amounts of labor, energy and time, and recognizing this might amplify, or further support the awesomeness triggered by the vast physical form. Vastness might also refer to extraordinary craftsmanship, such as speaks from the accuracy of the decorative stonework in the Alhambra (Spain), or from the technical/structural virtuosity necessary to construct a vaulting spanning a huge stretch of space in a medieval cathedral. It might refer to the use of materials that are notoriously difficult to collect or that are very labor intensive to work or process. Of course, all these processes need to be managed, and this managerial ability can itself be a source of awe when it takes on extraordinary proportions. A recent example is the Beijing Airport which was built at the occasion of the 2008 Olympic Games and took less than 4 years from plan to completion. The airport's physical scale is not only impressive, but it also represents an awesome display of bureaucratic efficiency.

It thus appears that there are two principal sources of vastness in RMA – and hence of awe—and these run along the same lines as the two perspectives brought together in our dual account of RMA. That is, (a) the direct perception of "bigness" can be a source of awe as much as (b) the costliness (i.e., wastefulness) underlying the construction of that bigness. Note however, that a certain amount of knowledge might be required to be awed by costly building activities (i.e., condition b). Consider the case of a tiny temple built atop a huge mountain. Although this temple might fulfill the physical vastness condition (i.e., a), because it is built on a high place, the building could be seen as a form of cheating because it derives its high position solely from the height of the mountain. However, learning/knowing that the mountaintop was absurdly inaccessible at the time of the construction of the temple might still fill one's experience of the building with awe. Probably, when both the physical size of the building (condition a) and the costly investments made to construct it (condition b) are impressive, and embodied in one and the same building, then it becomes very likely that an intense awe response to the building will occur. Notice that in the case of RMA, bigness often necessarily goes hand in hand with costliness. In the age of dazzling skyscrapers, it is easy to forget how difficult it was in the past to achieve great height. Without great width, depth and mass, massive structures often ran the risk of collapsing, as is illustrated—for example—by the case of the Notre Dame d'Amiens (France). In this cathedral, the flying buttresses were initially placed too high, and were barely able to counteract the lateral forces that came from the ceiling arch. First, this was resolved by placing lower buttresses, but when, after some time, cracks in the lower walls of the building began to appear, builders finally installed an iron bar chain running inside the walls, holding the cathedral together (Nova, 2012). This ex- ample clearly shows that it is difficult to exploit the sensitivity to bigness on the cheap. In the past, building high almost necessarily was a costly enterprise, requiring—among other things—technical ingenuity, large human labor investment and an abundance of material resources. One of the few "easy" ways in which height—or rather subjective impressions of height—could be in- creased was through illusion. In gothic cathedrals, for example, impressions of height are sometimes amplified by the (vertical) shafts running from the floor up to the ceiling. Other methods for creating the optical illusion of added height is to taper the walls of the monumental structure, or to paint the higher versus the lower parts in different shades (the higher the lighter the shade), like is the case in the Eifel Tower.[14]

Ever Higher.

If triggering dominance perceptions and awe experiences is indeed an important function of religious monumental buildings, it can be expected that their religious (or ideological) builders will have attempted to build as high as they were capable of. In agreement with this prediction, it appears that throughout history the achieved height of the world tallest buildings increased synchronously with the development of new engineering and technological skills (see Figure 2). However, apart from their pure height, also the height-to-width ratio of monumental buildings seems to have increased over time, probably stemming from an increased ability to overcome the technical limitations hampering building high structures. For example, the highest church in the world, the Ulm Minster (Ulm, Germany, 1890 AC, 161.5m) only slightly exceeds the Great Pyramid of Giza (2560 BC, 146.5m) in height, but it is far more slender than the pyramid, even though buttresses had to be added to keep the church building upright. Skyscrapers of the first decades of the 20th century, such as the New York Empire State Building (1931 AC, 381m), achieved approximately 2 times the height of the world's tallest churches, but with a similar height to width ratio. Finally, the height of the Burj Khalifa (2010 AC, 828m), a skyscraper in Dubai, doubles that of the Empire State Building, whereas its basis has approximately the same width.

Building Communities by Exploiting Awe

In a nutshell, in the previous sections, we argued that RMA exploits feelings of awe in spectators by being at the same time a costly signal and a structure that taps into our shared sensitivity to bigness. Having made this framework explicit, in the following sections, we will elucidate how awe experiences interlock with and promote religions' social function. In the first section, the role of awe in vertical social

[14] Note that male bowerbirds also use forced perspective in their bowers, possibly to appear bigger to females (cf., Endler, J. A., Endler, L. A., & Doerr, 2010).

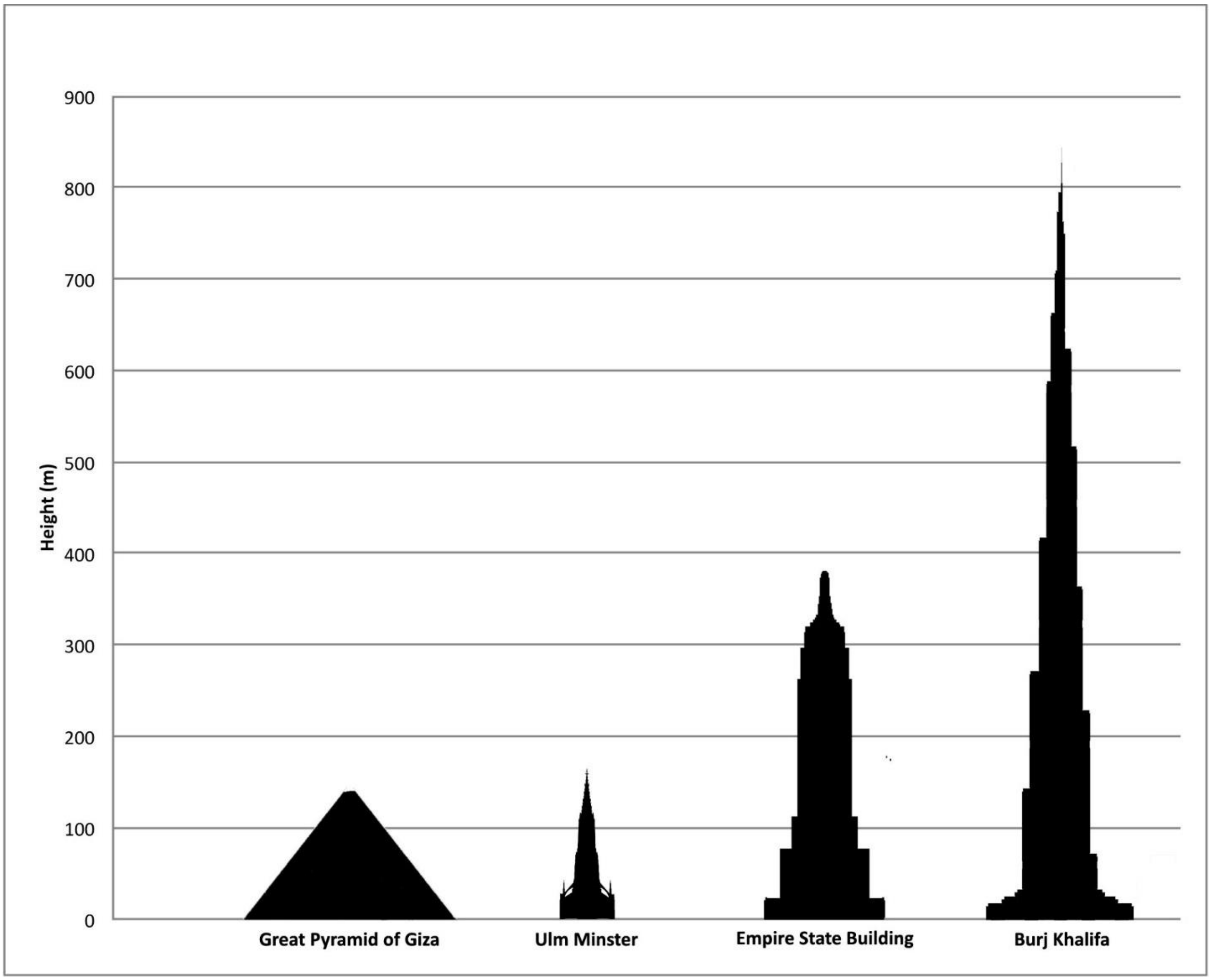

Figure 2. Heights of four of the world's tallest buildings throughout history.

stratification is discussed, and the second section touches upon the possible community building effects of experiencing this emotion. In the third section, we explain how RMA might have coordinated and monitored social life. Note that in these sections, we aim to shed light on the function(s) of RMA from the perspective of the (large-scale) religious community in which the instance of RMA was embedded. We do not exclude, however, that RMA might have had analogous functions for certain smaller groups or even for the particular individuals within those communities. Whereas RMA might be interpreted as a means of religious communities to yield prestige, it is of course entirely possible that RMA might also have increased individuals' own prestige because, for example, they actively contributed to building the structure. We refer to the discussion section for a further consideration of the possible consonances and conflicts between the functions of RMA on the group versus the individual level.

The Role of Religious Monumental Architecture in Vertical Social Stratification

There is ample evidence that in the presence of dominant individuals, or visual cues correlating with actual dominance, people are inclined to behave obediently or submissively. In the infamous obedience experiment by Milgram, for example, volunteers went so far as to give (seemingly) lethal electroshocks to a stranger because an authority figure (i.e., the experimenter) pressed them to do so (Milgram, 1963). Recent research demonstrates that watching individuals power posing (e.g., taken an open posture) leads to hormonal changes that correlate with submissive behavior (i.e., decrease in testosterone, increase in cortisol; Carney, Cuddy, & Yap, 2010). When individuals are faced with a dominant confederate, their submissive behavior is evident from the fact that they tend to adopt constricted postures (Tiedens & Fragale, 2003). A study by Fennis (2008) shows that individuals behave more submissively toward confederates when the latter surround or associate themselves with high status brands/products. Inasmuch as RMA can, by its size and height, be considered as an architectural embodiment of a dominant/powerful religious group or entity, the foregoing research suggests that commoners are prone to behave more obediently and submissively when faced with such grand edifices. Thus, as a signal tapping into the afore- mentioned sensitivity for bigness and its (emotional) effects (especially awe), RMA's physical appearance might have actively contributed to the process of vertical stratification and social ranking. This complements the costly signaling view on monumental architecture outlined earlier ("Monumental Architecture as a Costly Signal"). According to that view, social organization and stratification result from the building process, that is, from the recognition that the builders were capable of mobilizing and con- trolling large amounts of energy and labor (cf., Neiman, 1998).

It is important to note that the mechanism through which RMA has its socially stratifying effects probably deviates from that underlying dominance displays. During such displays, size cues (e.g., grandstanding) are also often employed, but the dominant individual—or the one trying to dominate—uses these to enforce a hierarchical relationship upon another individual. If RMA would play a closely analogous role, then it mainly would have functioned as a device for oppressing and intimidating people. If that were RMA's sole function, then it needs to be explained why instances of RMA are often also highly aestheticized, and are often attractive rather than merely oppressive. This suggests that such edifices also functioned to attract or "seduce" commoners, rather than to merely intimidate them (Huyssen, 1996).

It seems that by exploiting awe RMA can have it both ways. On the one hand, due to the fact that awe is primordially rooted in submissive feelings toward dominant individuals (Keltner & Haidt, 2003), RMA might tap into emotions related to submission. On the other hand, contrary to "pure" dominance displays, those feelings seem to be willingly conferred to the stimulus that provokes awe (cf., Henrich & Gil–White, 2001). Or as Frijda and Parrott (2011) put it: "Awe recognizes the power and quality of someone, some object, or some performance. One willingly and openly recognizes the target's superiority, refrains from competing, and from challenging the target's power" (p. 411). The sense of smallness and cognitive inadequacy that derive from perceiving the grandeur of RMA might thus define and consolidate hierarchical ranking, but that relationship seems primarily to result from freely "surrendering" to the awe-producing authority, rather than that it is caused by an attempt at (enforced) submission by that authority.

Religious monumental architecture is thus not solely intimidating and oppressive, but it can also deeply impress the (religious) spectator, being attractive rather than repellant. However, in addition to the vastness inherent to RMA, further particularities of the construction process and of the building's shape, can give RMA either a more oppressive or impressive/attractive "flavor." Appraisals of "oppressiveness" or "impressiveness" can derive from the building process itself. For example, throughout history constructing monumental architecture has frequently been a way of leaders to mercilessly oppress and dehumanize certain (ethnic) groups or minorities, like it happened in Hitler and Speer's monumental architecture program. The specific shape or layout of the building, or particular architectural features can however also bring about feelings of oppression versus impression. Oppressiveness can, for example, be due to including anxiety-inducing elements in RMA, such as sharp spires/towers or piercing forms (Larson, Aronoff, Sarinopoulos, & Zhu, 2009), dark enclosed spaces (Stamps, 2005), or representing threatening animals in ornament (Barrett, 2005). On the other hand, incorporating shiny and glistening surfaces (Coss, 2003), brightly colored architectural features (cf., gothic rose windows), or ornaments of nonthreatening elements might make a monumental structure attractive rather than intimidating.

The Role of Religious Monumental Architecture in Communal Bonding

Besides introducing and enacting social ranking and facilitating "vertical" attachment to religious leaders and deities, we conjecture that RMA is also capable of generating "horizontal" attachment, that is, increased bonding and attachment among religious followers. The actual physical appearance and geographical location of such buildings might already play a role in this process. Due to their massive scale, inside and around instances of RMA, there often is a lot of space for large groups of people to gather, providing ample opportunities for social interaction and social sharing. Medieval cathedrals, for example, are known to have served as civic gathering places or even marketplaces (Estabrook, 2002).

In addition to providing physical opportunities for gathering, we deem that by triggering awe, RMA can also psychologically facilitate social gathering/bonding. Examinations of the direct effects of awe suggest that this particular emotion indeed has community building potential by making people feel connected and act prosocially toward each other. Shiota and colleagues (2007), for example, discovered that experiencing awe causes people to feel as belonging to a large group, whereas this effect did not occur for other positive emotions, such as pride. Similarly, Saroglou, Buxant, and Tilquin (2008) found that watching awe-eliciting events/ scenes, such as natural scenery, made respondents feel more connected and committed to others, when compared with respondents who had seen an amusing video clip. Van Cappellen and Saroglou (in press) recently replicated this effect by showing that in spiritual/religious respondents, experiencing awe leads to sentiments of oneness with close others and with humanity as a whole, as opposed to experiencing humor. Awe makes people also more willing to spend their time on helping others (Rudd, Vohs, & Aaker, in press). Our own research findings are consistent with this and point out that exposure to natural, awe-evoking scenes makes people more inclined to act prosocially toward others, as compared with mundane natural scenes/elements (Joye & Bolderdijk, unpublished data).

Based on these empirical findings, we propose that RMA can exploit the social unification effects of awe, and as such, can also "horizontally" contribute to religious community building. Further research is needed, however, to uncover the exact mechanism responsible for this effect. Our own hypothesis is that the community-building effect of awe is driven by two interlocking psychological mechanisms, which directly tap into the two central features of awe experiences, proposed by Keltner and Haidt (2003), that is, vastness and need for accommodation.

A first mechanism is linked to the vast physical scale of these religious edifices. Research shows that priming individuals with large versus small spatial distances makes them frame and consider things in terms of more abstract mental representations or "construals" (e.g., "fruit" vs. "apple"; Henderson & Wakslak, 2010). Of particular interest for our argument is that Meyers–Levy and Zhu (2007) found that high versus low ceiling heights makes individuals classify objects into broader and more inclusive categories. In an analogous way, we conjecture that exposure to the massive scale and height of RMA will have made it more likely that religious followers represented fellow- followers in terms of a collective entity or group, rather than as a collection of separate individuals. This focus on the communal might be further reinforced by the fact that the highly attention-grabbing character of awe-triggering stimuli brings about a diminished sense of self in the viewer and a strong focus on external events and elements (Shiota et al., 2007).

However, neither focusing on others (instead of on oneself), nor viewing them in terms of a collectivity will necessarily motivate an individual to turn to or to attach to a group of individuals. A second mechanism which we identify (for community building) relates to the feeling of mental/cognitive inadequacy that might arise from perceiving the vastness inherent in RMA. Specifically, people are likely to turn to, or to rely on others to compensate for the sense of insignificance and (cognitive) uncertainty that can be caused by experiencing awesome events or elements (Derbaix & Vanhamme, 2003; Marigold, McGregor, & Zanna, 2009). In as much as RMA created—through awe—feelings of uncertainty and insignificance (cf., Griskevicius, Shiota, & Neufeld, 2010) and shook an individual's mental structures, a tendency for religious followers to "flock together" would have constituted a compensatory strategy to curb those feelings (for a review, see: Kay, Gaucher, McGregor, & Nash, 2010; Rucker & Galinsky, 2008).

The crux about the previous argument is that RMA exploits psychological dispositions closely interwoven with awe, which— indirectly—facilitate communal bonding. On the one hand, we assume that the subjective sense of (cognitive and physical) insignificance caused by RMA leads to a compensatory need for attachment to others. On the other hand, monumental architecture's massive spatial scale makes that people's representations of those others tend to transcend the level of "particular selves." Notice that this last conclusion dovetails with the proposition that in religions experiences of self-transcendence contribute to generating group cohesion (Durkheim, 1915). Self-transcendent states are commonly reached during ritual performances or acts, in which individuals participate in, for example, singing or synchronous rhythmic behavior. Research confirms that jointly making music (Kirschner & Tomasello, 2010) and moving synchronously (i.e., walking in step; Wiltermuth & Heath, 2009) leads to increased cooperation and helping behavior, which can foster communal living. As will be further discussed ("Religious Monumental Architecture as Context for Religious Activities and Rituals"), RMA should be viewed as being an integral part of, and supporting this ritual component of religious doctrines.

Religious Monumental Architecture as a Social Monitoring Device

Inevitably, religious communities are faced with the challenge of regulating communal/religious living. Without appropriate social monitoring, freeloaders might reap the benefits of the prosocial and cooperative efforts of fellow community members without them- selves complying to the social rules and norms. It has been hypothesized that religions have a number of built-in adaptive strategies to deal with problems of defection and freeloading. One proposal, made (among others) by Rossano (2007) is that ever-present supernatural beings are a means for social scrutiny, encouraging social cooperation among community members and, in so doing, consolidating social community living (see also: Alcorta & Sosis, 2005).

In religions, it is commonplace to use artifacts to remind people of the customary religious ethos (e.g., the cross in Christianity). Quite probably, instances of RMA will have played a similar social regulatory role (cf., Atran & Henrich, 2010). In so doing, such edifices complement the regulatory function of physically present social monitors (e.g., priests) and supernatural monitors (e.g., deities). Due to their massive scale, monumental constructions are often extraordinarily salient, grab and engage attention, and are therefore suited for regulating social/religious life across considerable spatial distances. Of further importance is that the interpretation of such "monumental monitors" does not depend on language, age, gender, or culture and that they can be simultaneously accessed by large groups of individuals, and this during different epochs (De Marrais et al., 1996; Alcorta & Sosis, 2005). We anticipate that exposure to awe-evoking RMA will have made it more probable that followers live up to the prosocial norms that are embodied in, or evoked by such buildings, as opposed to non-awe- provoking religious buildings. This is because awe involves an (implicit) recognition of the presence of a superior and highly powerful authority (Keltner & Haidt, 2003), almost literally looking down on religious followers and (implicitly) commanding them to live up to the prevailing social rules and norms.[15]

What is the mechanism through which such architectural monitoring could have taken place? Two pathways can be distinguished. A first one is directly related to the finding that priming individuals with religious concepts (e.g., "divine") makes them more inclined to conform to prosocial norms, and to behave and act more prosocially toward other members of their social group (that could also imply behaving nonsocially toward out-group members; see: Preston, Ritter, & Hernandez, 2010; cf., Shariff &

---

[15] It might be noted that there is a seeming contradiction between the "monumental monitors" idea and the claim that RMA should be under- stood in terms of a costly signal. Could it not be the case that the height of cases of RMA is merely a prerequisite for optimally performing the monitoring function? In other words, is RMA, considered from the perspective of monitoring, not just efficient design instead of strategically wasteful design? Against this, it can be pointed out that monitoring only seems to require that the structure stands out so much among surrounding (built) structures that it (significantly) enters the visual field. One often sees, however, that RMA is vastly higher than the surrounding buildings and fills a substantial portion of the visual field. Moreover, the use of elements which increase subjective impressions of height and the use of adornments and decorations, suggest that such edifices were not only intended to monitor commoners, but also to appear attractive to them.

Norenzayan, 2007; Saroglou, Corneille, & Van Cappellen, 2009; Pichon, Boccato, & Saroglou, 2007). Recent research confirms that similar prosocial effects can occur when religious buildings are employed as primes, rather than religious concepts (cf., Atran & Henrich, 2010). Specifically, Pichon and Saroglou (2009) found that when religiousness is primed by a church, people express to be more willing to help the homeless than when they are primed with a nonreligious building (i.e., a gymnasium). Meier, Hauser, Robinson, Friesen, and Schjeldahl (2007) also found that vertical space and upward position—both of which are typical to RMA—activate divinity-related cognitions, which, in turn, might make particular (pro)social norms salient.

A second possible pathway underlying monumental monitoring is that spectators actually associate, or attribute supernatural social agency to the monumental structure. This may make commoners feel as if being watched or monitored, thereby stimulating them to act and behave prosocially. This claim is in line with evidence showing that the presence of (minimal) social cues (e.g., eye spots) makes individuals behave more generously in economic games (Haley & Fessler, 2005) and more willing to donate to a good cause (Bateson, Nettle, & Roberts, 2006). Note that, consistent with this view, in different religions religious monumental buildings are assumed to be the dwelling places of supernatural beings. For example, the Egyptian word for temple—hwt-ntr—literally means "god's House" (Trigger, 1993).

Belief in the presence of divine agency in RMA could, of course, merely be an article of faith shared by many religions, which followers acquire after having become acquainted with the religious doctrine. However, it is also possible that attributing (supernatural) agency to monumental edifices is partially independent from the particular teachings of a doctrine. Being an intentionally made structure, RMA might already activate cortical net- works that lead to mental state attributions, even if the monumental structure does not contain any direct cues of social agency (Steinbeis & Koelsch, 2009). Those ascriptions of agency might get flavored with supernaturalness as a way to make the structure's mind-boggling grandeur and complexity more intelligible (cf., Bloom, 2007).

Note that monumental buildings can also contain, or be accompanied by visual features/elements that make spectators inclined to (implicitly) ascribe agency to RMA. Some cases of religious (monumental) architecture are, for example, adorned with human- like figures or are "guarded" by monumental statues (e.g., the Sphinx at Giza), whereas others contain eye-like schemas, such as, Imre Makovecz's church in Siófok or the stupa of the Swayambhunath buddhist temple in Kathmandu. Some (monumental) buildings from the classic Mayan period are even adorned with breath- ing imagery, suggesting that these constructions were in a sense alive (Saturno, Taube, Stuart, & Hurst, 2005). Given the finding that vertical upward motion is associated with animacy (Szego & Rutherford, 2008), the upward movement embodied in many in- stances of RMA can also be a trigger of perceptions of agency.

The observation that RMA has regularly been imbued with (supernatural) agency can perhaps expand one's understanding of why such type of building has also been a perennial target for destructive acts and why that destruction was often followed by violent retaliations. Within religious doctrines, the installment of new religious leaders often went hand in hand with cycles of demolishing and rebuilding RMA (sometimes even taking on ritual forms), which has been interpreted as a way of these (religious) elites to legitimize their newly obtained leadership, to cut commoners' ties with previous rulers and to create and strengthen new attachments. However, it is also very common for RMA to be attacked by external groups, belonging to rival ideologies and religions.[16] Consider for example the Taliban's dynamiting of the Buddha's of Bamyam (2001, Afghanistan) or the demolition of the Babri Mosque (1992, India) by Hindus. Of course, as being conspicuous religious symbols, cases of RMA might just be the "easiest" and most visible targets to eliminate. However, inasmuch as RMA is truly a materialization of supernatural agency, then destroying such buildings might be considered as an attempt to almost literally "kill" a religion's (supernatural) agents, and one of the most powerful (psychological) ways to try to wipe out the rival religious/ideological doctrine. Annihilating these monumental monitors may make followers to feel as being deserted by their deities, leading to widespread despair and vulnerability.

The fact that especially high monumental buildings are perceived as signaling devices of religious or ideological dominance is illustrated by the 9/11 attacks on the World Trade Center (WTC) towers in New York City. First, there is the remarkable fact that destroying the extraordinarily high towers of the WTC imposed such psychological distress on Americans, whereas they did not seem nearly as upset by the big hole blown in the horizontally expansive Pentagon—and perhaps they would not have, even if the Pentagon had been utterly destroyed. Second, the Twin Towers were perceived as quasi-religious monuments, both by attackers and the attacked. For example, Osama bin Laden declared that the attacks on the WTC were acts in a Muslim "holy war," that is, a religious war against the United States of America. Some American Christians, from their part, still tried to see traces of their god's presence in the remains

[16] The destruction of competitors' conspicuous signaling devices is not limited to the human species. The analogy we previously drew with bower construction applies here as well: in some bowerbird species males destroy bowers of competitors (Borgia 1985; Borgia & Müller 1992).

of the buildings after the attacks. Specifically, the steel beams shaped like a cross which were discovered in the aftermath of the 9/11 attacks by a worker from the rubble at Ground Zero (New York) were seen as “a sign that God never abandoned us at Ground Zero” (Reuters, 2011).

Religious Monumental Architecture Builds Religious Beliefs by Exploiting Awe

Up to now, we have said little to nothing about the beliefs which permeate religious communities. In the cognitive science of religion, religious beliefs are often considered to be beliefs in super- natural agents. One influential view is that belief in such agents is similar to attributing intentional agency to simple geometric shapes moving on a screen (Heider & Simmel, 1944), which amounts to little more than a misapplication of mental modules for detecting agency (Barrett, 2000; Atran & Norenzayan, 2004). In the ensuing sections, we explore how feelings of awe, triggered by RMA, might have influenced and interacted with the process of adopting supernatural beliefs. In the first section, we argue that RMA can create ideological/religious openness in followers, whereas the second section discusses how, as being a signal of religious commitment, such architecture can further support the process of religious belief adoption. Notice that the community perspective still constitutes the backdrop of this exploration. That is, belief commitment is deemed to actually support or reinforce the social function of religions (for a discussion, see, e.g., Atran & Henrich, 2010).

Religious Monumental Architecture Creates Ideological Openness

Keltner and Haidt (2003) conjecture that feeling awe can foster (religious) belief adoption and/or ideological transformation. Research by Shiota and colleagues (2007) supports this claim by showing that individuals with a high disposition to experience awe are indeed more willing to revise their mental structures, or to admit their inadequacy, as compared with individuals who have a high disposition for other positive emotions (i.e., dispositional pride and joy). The impact of experiencing awe on spirituality and religious openness has been directly investigated in a few experiments. A qualitative ethnographic study among wildlife tourists by Curtin (2009), for example, reveals that experiencing awe and wonderment, caused by watching wildlife, sparks spiritual feelings in participants. Research by Saroglou and colleagues (2008) points out that respondents score higher on spirituality measures after having watched an awe-eliciting video (e.g., involving nature scenery, among others) rather than a comedy, or an emotionally neutral video. When recalling an awe-evoking event, religious/ spiritual people are also more inclined to undertake a journey to a spiritual destination (i.e., Tibet) than to a hedonic destination (i.e., Haiti) as opposed to respondents recalling an event triggering pride (Van Cappellen & Saroglou, 2012).

If, as the foregoing findings seem to suggest, awe can indeed foster ideological/religious openness, then RMA can be interpreted as an artful device to make the minds of potential followers more open to the religious beliefs that are preached in, or associated with such religious contexts. This ideological/religious openness might subsequently make (potential) followers to actually take up particular supernatural, and hence, inherently counterintuitive concepts, beliefs or narratives (Norenzayan, Atran, Faulkner, & Schaller, 2006). Note that this effect was clearly exploited in reformation Europe (among others). As Brown (2004) documents, during that epoch the papal patrons appointed artistic geniuses like Bernini and Michelangelo to create awesome architectural spaces, such as the Saint Peter's Cathedral in Rome, in an attempt to further propagate the faith.

What is the possible mechanism through which cases of awe-provoking RMA might promote ideological/religious openness? Probably, this relates to the fact that when experiencing awe one's available mental frameworks prove to be inadequate for fully grasping the object or event that triggers awe (Keltner & Haidt, 2003). Due to a compensatory need to update or revise those frameworks, individuals might become more willing to embrace new or alternative beliefs/frameworks that enable them to surmount this mental inadequacy (Shiota et al., 2007; Kay et al., 2010). At the same time, this cognitive inadequacy is caused by structures that transcend the scale and complexity of common built accomplishments to the highest degree. This probably makes people more open to invoke supernatural beliefs into the process of cognitive accommodation, or tips them into believing that the building cannot be other than the work of the god(s) (Bloom, 2007), as compared with smaller, hence, non-awe-provoking religious buildings.

Religious Monumental Architecture Illustrates Belief Commitment

The picture emerging from the previous section is that cases of awe-inducing RMA can instill ideological openness in religious followers. Of course, the transition from being open to a set of religious beliefs to actually adopting those particular beliefs depends on many factors. For example, when individuals have experienced awe, they appear to process messages more deeply rather than heuristically, with the result that weak propositions are considered as substantially weaker than when they have experienced other positive emotions (e.g., amusement; Griskevicius et al., 2010). The implication is that awesome RMA might foster openness to religious beliefs, but only those beliefs that are backed up by sufficiently “strong arguments” will be favored and retained. There are probably a number of “context biases” that mediate the relationship between ideological openness and actual belief adoption. For example, given the influence of prestige signals on social learning (Richerson & Boyd, 2005), beliefs that are endorsed by prestigious individuals have more chance of being retained by learners than those that do not have such endorsement.

Although we do not have the intention to provide an exhaustive review of possible mediating factors, we would like to touch upon one potential characteristic— often intrinsic to RMA – that can facilitate the transition from ideological openness to actual religious belief adoption. Following Henrich (2009), religious monumental buildings can be interpreted as illustrating the principle of “actions speak louder than words” (Gervais & Henrich, 2010; Atran & Henrich, 2010). Specifically, Henrich (2009) argues that learners should be more willing to overtake beliefs from religious models (e.g., priests) who support their (supernatural) beliefs with acts or behavior that demonstrate that they are actually committed to those beliefs, than from models who just verbally or symbolically express those beliefs. Individuals will, for example, be more inclined to take over a prestigious individual’s belief in altruism when (s)he backs this belief up by donating money to a good cause, rather than when (s)he merely preaches that belief.

Although specific religious practices (e.g., ritual bloodletting) are often considered as key examples of such “credibility enhancing displays” (CREDs; Henrich, 2009), constructing monumental architecture might be another way to demonstrate religious belief commitment (cf., Atran & Henrich, 2010). Religious leaders/ institutions, but also members of the general population who physically or financially contributed to constructing such edifices (e.g., through taxation), illustrated by this toward potential followers or fellow followers that they were actually committed to particular supernatural beliefs. Therefore, belief structures backed up by monumental building achievements have more chance of being overtaken from models than beliefs that are not, or are to a lesser degree supported by such accomplishments. When RMA not only produced ideological openness through awe (see “Religious Monumental Architecture Creates Ideological Openness”), but at the same time, also represented a reliable signal of commitment to those ideas, then this might have been the kind of “strong argument” (cf., Griskevicius et al., 2010) that could further stabilize or “fix” religious beliefs in the minds of followers, which ultimately contributed to religious steadfastness. In other words, when an awe-evoking instance of RMA also was a CRED, then this might have bolstered actual adoption of, and commitment to the associated supernatural beliefs. Thus, in addition to the fact that creating height in RMA was costly due to constructional/technical limitations (see

"Religious Monumental Architecture Exploits Awe"), the foregoing argument suggests that costliness might also be required for strengthening belief commitment.

Religious Monumental Architecture as Context for Religious Activities and Rituals

Up until now we have mainly considered RMA as an isolated phenomenon. It needs to be noted, however, that the emotional impact of these religious structures also depends on, and interacts with the specific activities that are/were performed in or near them. Specifically, rather than standing on its own, this type of architecture should be viewed as being part and parcel of, and supporting the ritual component of religious doctrines (De Marrais et al., 1996). But how should this cross-fertilization between rituals and RMA be conceived? On the one hand, the emotional impact of a monumental religious building might have been further intensified or colored by the fact that such edifices regularly were the stage of rituals or ritualistic activities, and were an intrinsic part of a network of religious beliefs (Alcorta & Sosis, 2005). Such "supplementary" emotional charging might have been particularly important when, after repeated exposure, habituation to RMA would kick in, diminishing the intensity of the original awe response (Haidt, Seder, & Kesebir, 2008).

On the other hand, by causing awe, RMA might also have emotionally charged particular religious (ritual) activities, beliefs, or narratives. For example, due to conditioned association, beliefs voiced in or near monumental religious contexts could have become further emotionally loaded and sanctified, reinforcing their regulative and coordinative function (Alcorta & Sosis, 2005). Research furthermore indicates that beliefs or messages that are arousing (Berger, 2011), or that trigger strong emotions, such as disgust (Nichols, 2006; Heath, Bell, & Sternberg, 2001), awe (Berger & Milkman, 2011) or surprise (Derbaix & Vanhamme, 2003), have a mnemonic advantage over beliefs/norms that have less emotional salience. Together, these findings suggest that, in as much as beliefs or religious messages can be embodied in, or communicated by the overall building, beliefs exemplified in awe-evoking RMA will have had a mnemonic, and hence, transmission advantage over beliefs exemplified in more mundane religious structures.

In addition, by providing a physical context for performing or attending rituals, such emotionally arresting environments might have made that the rituals or religious happenings, and the specific messages/beliefs implied in those, became more firmly anchored in the minds of participants. For example, as certain rituals functioned to initiate or reinforce belief commitment, awe-evoking contexts will have further emotionally colored such happenings, and in so doing, contributed to making such episodes more memorable. This is nicely illustrated in one of the key-scenes of the film *Apocalypto* (2006, Mel Gibson), where the powerful emotional impact of Mayan ritual human killings is amplified by the fact that these take place on top of monumental pyramids. Such dramatic monumental backgrounds probably made it more likely that followers "kept the faith" and increased the chances that such beliefs became transmitted in the religious community. Monumental architecture thus seems to be part and parcel of what Whitehouse coins the "imagistic" component of religious systems (Whitehouse, 2004). In this mode, remembering religious beliefs and vows does not so much depend on repeated learning of central aspects of the doctrine (i.e., the "doctrinal" component), but it rather follows from partaking in highly arousing events.

Finally, notice that in our view, RMA is—initially—not emotionally neutral, as opposed to, for example, water which has been turned into holy water during ritual practices (Alcorta & Sosis, 2005). Such edifices rather seem to play on preexisting, and possibly prewired emotional/aesthetic sensitivities (e.g., sensitivity to bigness). A concern might be that our argument was mainly built around two "structural" features of awe (i.e., vastness and cognitive inadequacy; cf., Keltner & Haidt, 2003), but remained largely silent about the specific emotional valence of awe-evoking instances of RMA. In recent discussions awe is commonly considered as a positive emotion (cf., Griskevicius et al., 2010). However, in as much as this emotion, and the elements which are able to trigger it, encompass mental inadequacy or insignificance, awe can also have some negative loading. In addition, and as already mentioned ("The Role of Religious Monumental Architecture in Vertical Social Stratification"), RMA can exhibit characteristics, unrelated to the two central features of awe, which further emotionally "flavor" the experience of the awe-provoking structure, in positive as well as in negative ways. This might, in turn, amplify some of the proposed effects of RMA. For example, the dark and shadowy interior of a particular instance of RMA can flavor the experience of awe with fear (Keltner & Haidt, 2003), through which potential freeloaders might become more strongly motivated to behave prosocially, as compared with RMA that has no such flavoring (Alcorta & Sosis, 2005).

Discussion

In this chapter, we attempted to demonstrate that a Darwinian approach can shed light on (some of) the evolved functions of architecture, and of RMA, in particular. We started our argument with a discussion of Trigger (1990) and Neiman's (1998) account of monumental architecture, according to which the costliness of such building accomplishments signals the competitive ability of their elite builders. Our dual account of RMA extends Neiman's costly signaling account in three respects. First, in addition to costly signaling theory, we invoked sensory exploitation theory to more fully explain particular formal characteristics of

RMA. Specifically, in RMA there is a perennial tendency to express costliness/ wastefulness through height, and we interpreted this as a way of RMA to exploit the adaptive tendency to associate height and size with power and dominance (i.e., “sensitivity to bigness”). Second, we challenged the view that RMA’s evolved function can solely be grasped from the perspective of sexual selection (cf., Neiman, 1998). Rather than signaling the “good genes” of their builders, such buildings can also be interpreted as prestige signals that, once picked up by social learners, galvanize cultural evolution. Third, our framework extends common accounts of RMA in that it gives center stage to the emotional impact of RMA. In particular, the emotion of “awe” was considered as one of the most typical emotional responses to the two different types of vastness inherent in RMA, that is, vastness in size and vastness in effort.

Once the theoretical structure of our model was spelled out, we argued that RMA – being understood as a (culturally) evolved device for inducing awe—served four interrelated functions in religious communities: to contribute to vertical stratification; to facilitate bonding between religious community members; to monitor religious/social life across time and space; and to create ideological/religious openness in the religious population. Notice that it is very probable that (some of) these hypothesized functions of RMA are also being exploited in secular contexts by monumental nonreligious built structures, such as corporate skyscrapers, government buildings, courthouses, banks, sports stadia, airports, railway stations, statues or even virtual constructions in video games.

In this chapter, religion was considered as a culturally evolved device that help(ed) creating, regulating and enacting (large-scale) community living. Our purpose was to look at how far we could understand the physical appearance of RMA, as well as the wasteful processes underlying that appearance, from that social perspective. We want to stress, however, that besides this social function, RMA might have had, or obtained functions which are largely unrelated to that community perspective. Building a massive religious edifice provided an occasion for many parties to gain a little more money, prestige, and glory for themselves, regardless of the monumental building’s religious content and symbolism. For example, in the context of medieval cathedral building the apprentice stone-mason promoted to master mason might have attracted a mate, impressed by his wonderful gargoyles or flying buttress details. The head priest of the religious monumental building might consider the structure not only as a way to strengthen community solidarity, but also as a means to increase his own prestige, and his influence and authority over commoners.

Our exploration of the social function of RMA was situated at intersection of religious doctrines and the religious communities associated with them. It must be clear however that instances of RMA are at the nexus of very complex, shifting, multigenerational networks of people, families, groups, (rival) ideologies, each trying to nudge the benefits of RMA in their own favor. With its focus on the group level our chapter has mapped only a fraction of that complexity. We hope that future research will further unravel the possible (evolved) functions of RMA obtained for these other stakeholders.

It is furthermore very much possible that the community function of RMA sometimes conflicted with other (individual and group) levels and interests. For example, religious/ideological leaders might have tried to increase their own prestige and that of their communities by pushing for ever bigger monumental buildings, which were however beyond what the population could bear in terms of taxation and labor. Not only might this have made followers turn against their leaders, when there were insufficient monetary or physical resources to complete the monumental building it might have become a source of (ingroup and outgroup) ridicule and embarrassment, rather than a source of communal pride and bonding. The still unfinished, and 330 m high Ryugyong Hotel in North Korea, whose building started during the Cold War, is perhaps one striking example of monumental architecture gone awry.

The research that was presented in this chapter can be viewed as being part and parcel of a broader research agenda that tries to map out why human minds generate religious beliefs. How do we construct such beliefs, why do we accept them, how do we spread them, and how can they cause otherwise rational human beings to be murderous in the name of supernatural agents? Against this particular research background, we hope that our exploration of the (culturally) evolved functions of RMA provides an addition to the field of religious studies. We are furthermore confident that our argument also illustrates that an evolutionary approach to architecture can offer valuable insights into the emergence, persistence and occurrence of particular types of architecture.

References

Alcorta, C., & Sosis, R. (2005). Ritual, emotion, and sacred symbols: The evolution of religion as an adaptive complex. *Human Nature, 16,* 323– 359. doi:10.1007/s12110-005-1014-3

Aranyosi, E. F. (1999). Wasteful advertising and variance reduction: Darwinian models for the significance of nonutilitarian architecture. *Journal of Anthropological Archaeology, 18,* 356–375. doi:10.1006/jaar.1999 .0346

Armstrong, T., & Detweiler–Bedell, B. (2008). Beauty as an emotion: The exhilarating prospect of mastering a challenging world. *Review of General Psychology, 12,* 305–329. doi:10.1037/a0012558

Arnqvist, G. (2006). Sensory exploitation and sexual conflict. *Philosophical Transactions of the Royal Society of London - Series B, 361,* 375–386. doi:10.1098/rstb.2005.1790

Atran, S., & Henrich, J. (2010). The evolution of religion: How cognitive by-products, adaptive learning heuristics, ritual displays, and group competition generate deep commitments to prosocial religions. *Biological Theory, 5,* 18–30. doi:10.1162/BIOT_a_00018

Atran, S., & Norenzayan, A. (2004). Religion's evolutionary landscape: Counterintuition, commitment, compassion, communion. *Behavioral and Brain Sciences, 27,* 713–730. doi:10.1017/S0140525X04000172

Barrett, H. C. (2005). Adaptations to predators and prey. In D. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 200–223). Hoboken, NJ: Wiley.

Barrett, J. L. (2000). Exploring the natural foundations of religion. *Trends in Cognitive Sciences, 4,* 29–34. doi:10.1016/S1364-6613(99)01419-9

Bateson, M., Nettle, D., & Roberts, G. (2006). Cues of being watched enhance cooperation in a real-world setting. *Biology Letters, 2,* 412– 414. doi:10.1098/rsbl.2006.0509

Berger, J. (2011). Arousal increases social transmission of information. *Psychological Science, 22,* 891–893. doi:10.1177/0956797611413294

Berger, J., & Milkman, K. (2011). Social transmission, emotion, and the virality of online content. *Wharton School Working Paper*. Retrieved from http://marketing.wharton.upenn.edu/documents/research/virality .pdf

Bloom, P. (2007). Religion is natural. *Developmental Science, 10,* 147– 151. doi:10.1111/j.1467-7687.2007.00577.x

Borgia, G. (1985). Bower destruction and sexual competition in the satin bowerbird (Ptilonorhynchus violaceus). *Behavioral Ecology and Sociobiology, 18,* 91–100. doi:10.1007/BF00299037

Borgia, G., & Müller, U. (1992). Bower destruction, decoration stealing and female choice in the spotted bowerbird (Chlamydera maculata). *Emu, 92,* 11–18. doi:10.1071/MU9920011

Brown, R. E. (2004). The propagation of awe: Public relations, art and belief in Reformation Europe. *Public Relations Review, 30,* 381–389. doi:10.1016/j.pubrev.2004.08.015

Carney, D. R., Cuddy, A. J. C., & Yap, A. J. (2010). Power posing: Brief nonverbal displays affect neuroendocrine levels and risk tolerance. *Psychological Science, 21,* 1363–1368. doi:10.1177/0956797610383437

Coss, R. G. (2003). The role of evolved perceptual biases in art and design. In E. Voland, & K. Grammer (Eds.), *Evolutionary aesthetics* (pp. 69– 130). Heidelberg, Germany: Springer-Verlag.

Curtin, S. (2009). Wildlife tourism: The intangible, psychological benefits of human-wildlife encounters. *Current Issues in Tourism, 12,* 451–474. doi:10.1080/13683500903042857

De Marrais, E., Castillo, L. J., & Earle, T. (1996). Ideology, materialization, and power strategies. *Current Anthropology, 37,* 15–31. doi: 10.1086/204472

Derbaix, C., & Van Hamme, J. (2003). Inducing word-of-mouth by eliciting surprise – a pilot investigation. *Journal of Economic Psychology, 24,* 99–116. doi:10.1016/S0167-4870(02)00157-5

De Waal, F. B. M. (1982). *Chimpanzee politics: Power and sex among apes*. London, UK: Jonathan Cape.

Durkheim, E. (1915). *The elementary forms of the religious life*. New York, NY: Free Press.

Ekman, P. (1992). An argument for basic emotions. *Cognition and Emotion, 6,* 169–200. doi:10.1080/02699939208411068

Endler, J. A. (1992). Signals, signal conditions, and the direction of evolution. *The American Naturalist, 139,* 125–153. doi:10.1086/285308

Endler, J. A., Endler, L. A., & Doerr, N. R. (2010). Great bowerbirds create theaters with forced perspective when seen by their audience. *Current Biology, 20,* 1679–1684. doi:10.1016/j.cub.2010.08.033

Estabrook, C. B. (2002). Ritual, space, and authority in seventeenth century English cathedral cities. *Journal of Interdisciplinary History, 32,* 593–620. doi:10.1162/002219502317345529

Fennis, B. M. (2008). Branded into submission: Bran attributes and hierarchisation behavior in same-sex and mixed-sex dyads. *Journal of Applied Social Psychology, 38,* 1993–2009. doi:10.1111/j.1559-1816.2008 .00377.x

Fiske, A. P. (1992). The four elementary forms of sociality: Framework for a unified theory of social relations. *Psychological Review, 99,* 689–723. doi:10.1037/0033-295X.99.4.689

Francis, L. J., Williams, E., Annis, J., & Robbins, M. (2008). Understanding Cathedral visitors: Psychological type and individual differences in experience and appreciation. *Tourism Analysis, 13,* 71–80. doi:10.3727/ 108354208784548760

Frijda, N. H., & Parrott, W. G. (2011). Basic emotions or ur-emotions? *Emotion Review, 3,* 406–415. doi:10.1177/1754073911410742

Fuller, R. C., Houle, D., & Travis, J. (2005). Sensory bias as an explanation for the evolution of mate preferences. *American Naturalist, 166,* 437– 446. doi:10.1086/444443

Gagnon, S. A., Brunyé, T. T., Robin, C., Mahoney, C. R., & Taylor, H. A. (2011). High and mighty: Implicit associations between space and social status. *Frontiers in Psychology, 2,* 259.

Gervais, W., & Henrich, J. (2010). The Zeus problem: Why representational content biases cannot explain faith in Gods. *Journal of Cognition and Culture, 10,* 383–389. doi:10.1163/156853710X531249

Giessner, S. R., & Schubert, T. W. (2007). High in the hierarchy: How vertical location and judgments of leaders' power are interrelated. *Organizational Behavior and Human Decision Processes, 104,* 30–44. doi:10.1016/j.obhdp.2006.10.001

Goodall, J. (1986). *The chimpanzees of Gombe*. Cambridge, MA: Harvard University Press.

Graham, J., & Haidt, J. (2010). Beyond beliefs: Religions bind individuals into moral communities. *Personality and Social Psychology Review, 14,* 140–150. doi:10.1177/1088868309353415

Griskevicius, V., Shiota, M. N., & Neufeld, S. L. (2010). Influence of different positive emotions on persuasion processing: A functional evolutionary approach. *Emotion, 10,* 190–206. doi:10.1037/a0018421

Haidt, J., & Algoe, S. (2004). Moral amplification and the emotions that attach us to saints and demons. In J. Greenberg, S. L. Koole,, & T. Pyszczynski (Eds.), *Handbook of experimental existential psychology* (pp. 322–335). New York, NY: Guilford.

Haidt, J., & Keltner, D. (1999). Culture and facial expression: Open-ended methods find more expressions and a gradient of recognition. *Cognition and Emotion, 13,* 225–266. doi:10.1080/026999399379267

Haidt, J., & Keltner, D. (2002). Awe/responsiveness to beauty and excellence. In C. Peterson, & M. E. P. Seligman (Eds.), *The VIA taxonomy of strengths. Cincinnati,* OH: Valves in Action Institute.

Haidt, J., Seder, P., & Kesebir, S. (2008). Hive Psychology, Happiness, and Public Policy. *Journal of Legal Studies, 37,* S133–S156.

Haley, K. J., & Fessler, D. M. T. (2005). Nobody's watching? Subtle cues affect generosity in an anonymous economic game. *Evolution and Human Behavior, 26,* 245–256. doi:10.1016/j.evolhumbehav.2005.01.002

Heath, C., Bell, C., & Sternberg, E. (2001). Emotional selection in memes: The case of urban legends. *Journal of Personality and Social Psychology, 81,* 1028–1041. doi:10.1037/0022-3514.81.6.1028

Heider, R., & Simmel, M. (1944). An experimental study of apparent behavior. *The American Journal of Psychology, 57,* 243–259. doi: 10.2307/1416950

Hejmadi, A., Davidson, R., & Rozin, P. (2000). Exploring Hindu indian emotion expressions: Evidence for accurate recognition by Americans and Indians. *Psychological Science, 11,* 183–187. doi:10.1111/1467- 9280.00239

Henderson, M. D., & Wakslak, C. L. (2010). Over the hills and far away: The link between physical distance and abstraction. *Current Direc tions in Psychological Science, 19,* 390 –394. doi:10.1177/ 0963721410390802

Henrich, J. (2009). The evolution of costly displays, cooperation and religion: Credibility enhancing displays and their implications for cultural evolution. *Evolution and Human Behavior, 30,* 244–260. doi: 10.1016/j.evolhumbehav.2009.03.005

Henrich, J., & Gil–White, F. J. (2001). The evolution of prestige: Freely conferred status as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior, 22,* 165–196. doi: 10.1016/S1090-5138(00)00071-4

Hersey, G. (1999). *The monumental impulse: Architecture's biological roots*. Cambridge, MA: MIT Press.

Huang, L., Galinsky, A. D., Gruenfeld, D. H., & Guillory, L. E. (2011). Powerful postures versus powerful roles: Which is the proximate correlate of thought and behavior? *Psychological Science, 22,* 95–102. doi:10.1177/0956797610391912

Huyssen, A. (1996). Monumental seduction. *New German Critique, 69,* 181–200. doi:10.2307/488614

Johansen, P. G. (2004). Landscape, monumental architecture, and ritual: A reconsideration of the South Indian ashmounds. *Journal of Anthropological Archaeology, 23,* 309–330. doi:10.1016/j.jaa.2004.05.003

Judge, T. A., & Cable, D. M. (2004). The effect of physical height on workplace success and income: Preliminary Test of a theoretical model. *Journal of Applied Psychology, 89,* 428–441. doi:10.1037/0021-9010 .89.3.428

Kay, A. C., Gaucher, D., McGregor, I., & Nash, K. (2010). Religious belief as compensatory control. *Personality and Social Psychology Review, 14,* 37–48. doi:10.1177/1088868309353750

Keltner, D., & Haidt, J. (2003). Approaching awe, a moral, spiritual, and aesthetic emotion. *Cognition and Emotion, 17,* 297–314. doi:10.1080/ 02699930302297

Kirschner, S., & Tomasello, M. (2010). Joint music making promotes prosocial behavior in 4-year-old children. *Evolution and Human Behavior, 31,* 354–364. doi:10.1016/j.evolhumbehav.2010.04.004

Kolb, M. J. (1994). Monumentality and the rise of religious authority in precontact Hawai'i social evolution. *Current Anthropology, 35,* 521– 547. doi:10.1086/204315

Larson, C. L., Aronoff, J., Sarinopoulos, I. C., & Zhu, D. C. (2009). Recognizing threat: Simple geometric shapes activate neural circuitry underlying threat detection. *Journal of Cognitive Neuroscience, 21,* 1523–1535. doi:10.1162/jocn.2009.21111

Marigold, D. C., McGregor, I., & Zanna, M. P. (2009). Defensive conviction as emotion regulation: Goal mechanisms and interpersonal implications. In R. M. Arkin, K. C. Oleson,, & P. J. Carroll (Eds.), *Handbook of the uncertain self* (pp. 232–248). New York, NY: Psychology Press.

Marsh, A. A., Henry, H. Y., Schechter, J. C., & Blair, R. J. R. (2009). Larger than life: Humans' nonverbal status cues alter perceived size. *Public Library of Science, ONE, 4,* e5707.

Meier, B. P., Hauser, D. J., Robinson, M. D., Friesen, C. K., & Schjeldahl, K. (2007). What's "up" with God? Vertical space as a representation of the divine. *Journal of Personality and Social Psychology, 93,* 699–710. doi:10.1037/0022-3514.93.5.699

Meyers-Levy, J., & Zhu, R. (2007). The influence of ceiling height: The effect of priming on the type of processing people use. *Journal of Consumer Research, 34,* 174–186. doi:10.1086/519146

Mignault, A., & Chauduri, A. (2003). The many faces of a neutral face: Head tilt and perception of dominance and emotion. *Journal of Nonverbal Behavior, 27,* 111–132. doi:10.1023/A:1023914509763

Milgram, S. (1963). Behavioral study of obedience. *The Journal of Abnormal Psychology, 67,* 371–378. doi:10.1037/h0040525

Miller, G. (2000). *The mating mind*. New York, NY: Penguin.

Moeller, S. K., Robinson, M. D., & Zabelina, D. L. (2008). Personality dominance and preferential use of the vertical dimension of space: Evidence from spatial attention paradigms. *Psychological Science, 19,* 355–361. doi:10.1111/j.1467-9280.2008.02093.x

Neiman, F. (1998). Conspicuous consumption as wasteful advertising: A Darwinian perspective on spatial patterns in Classic Maya terminal monument dates. In C. M. Barton, & G. A. Clark (Eds.), *Rediscovering Darwin: Evolutionary theory in archaeological explanation* (pp. 267– 290). Arlington, VA: American Anthropological Association.

Nichols, S. (2002). On the genealogy of norms: A case for the role of emotion in cultural evolution. *Philosophy of Science, 69,* 234–255. doi:10.1086/341051

Norenzayan, A., Atran, S., Faulkner, J., & Schaller, M. (2006). Memory and mystery: The cultural selection of minimally counterintuitive narratives. *Cognitive Science, 30,* 531–553.

Nova (2012). *Building the great cathedrals*. Retrieved from http://www .pbs.org/wgbh/nova/ancient/building-gothic-cathedrals.html

Pichon, I., Boccato, G., & Saroglou, V. (2007). Nonconscious influences of religion on prosociality: A priming study. *European Journal of Social Psychology, 37,* 1032–1045. doi:10.1002/ejsp.416

Pichon, I., & Saroglou, V. (2009). Religion and helping: Impact of target thinking styles and just-world beliefs. *Archive for the Psychology of Religion, 31,* 215–236.

Preston, J. L., Ritter, R. S., & Hernandez, J. I. (2010). Principles of religious prosociality: A review and reformulation. *Social and Personality Psychology Compass, 4,* 574–590. doi:10.1111/j.1751-9004.2010 .00286.x

Reuters (2011). *Steel girders shaped like cross headed back to Ground Zero*. Retrieved from: http://www.reuters.com/article/2011/07/18/ussept11- museum-cross-idUSTRE76H5ZG20110718

Richerson, P. J., & Boyd, R. (2005). *Not by genes alone: How culture transformed human evolution*. Chicago, IL: University of Chicago Press.

Rodd, F. H., Hughes, K. A., Grether, G. F., & Baril, C. T. (2002). A possible non-sexual origin of mate preference: Are male guppies mimicking fruit? *Proceedings Biological Sciences/The Royal Society of London B, 269,* 475–481. doi:10.1098/rspb.2001.1891

Rodriguez, R. L., & Snedden, W. (2004). On the functional design of mate preferences and receiver biases. *Animal Behaviour, 68,* 427–432. doi: 10.1016/j.anbehav.2003.08.031

Rossano, M. J. (2007). Supernaturalizing social life: Religion and the evolution of human cooperation. *Human Nature, 18,* 272–294. doi: 10.1007/s12110-007-9002-4

Rucker, D., & Galinsky, A. D. (2008). Desire to acquire: Powerlessness and compensatory consumption. *Journal of Consumer Research, 35,* 257–267. doi:10.1086/588569

Rudd, M., Vohs, K. D., & Aaker, J. (In press). Awe expands people's perception of time, alters decision making, and enhances well-being. *Psychological Science*.

Ryan, M. J. (1998). Sexual selection, receiver biases, and the evolution of sex differences. *Science, 281,* 1999–2003. doi:10.1126/science.281 .5385.1999

Saroglou, V., Buxant, C., & Tilquin, J. (2008). Positive emotions as leading to religion and spirituality. *The Journal of Positive Psychology, 3,* 165–173. doi:10.1080/17439760801998737

Saroglou, V., Corneille, O., & Van Cappellen, P. (2009). "Speak, Lord, your servant is listening": Religious priming activates submissive thoughts and behaviors. *International Journal of the Psychology of Religion, 19,* 143–154. doi:10.1080/10508610902880063

Saturno, W. A., Taube, K. A., Stuart, D., & Hurst, H. (2005). The murals of San Bartolo, El Petén, Guatemala, Part 1: The north wall. *Ancient America*, *7*.

Schubert, T. (2005). Your highness: Vertical positions as perceptual symbols of power. *Journal of Personality and Social Psychology, 89,* 1–21. doi:10.1037/0022-3514.89.1.1

Schubert, T. W., Waldzus, S., & Giessner, S. R. (2009). Control over the association of power and size. *Social Cognition, 27,* 1–19. doi: 10.1521/soco.2009.27.1.1

Schwartz, B., Tesser, A., & Powell, E. (1982). Dominance cues in nonverbal behavior. *Social Psychology Quarterly, 45,* 114–120. doi:10 .2307/3033934

Sergio, F., Blas, J., Blanco, G., Tanferna, A., López, L., Lemus, J. A., & Hiraldo, F. (2011). Raptor nest decorations are a reliable threat against conspecifics. *Science, 331,* 327–330. doi:10.1126/science.1199422

Shariff, A. F., & Norenzayan, A. (2007). God is watching you: Priming god concepts increases prosocial behavior in an anonymous economic game. *Psychological Science, 18,* 803– 809. doi:10.1111/j.1467-9280.2007 .01983.x

Shiota, M., Keltner, D., & Mossman, A. (2007). The nature of awe: Elicitors, appraisals, and effects on self-concept. *Cognition and Emotion, 21,* 944–963. doi:10.1080/02699930600923668

Stamps, A. (2005). Visual permeability, locomotive permeability, safety and enclosure. *Environment and Behavior, 37,* 587–619. doi:10.1177/ 0013916505276741

Steinbeis, N., & Koelsch, S. (2009). Understanding the intentions behind man-made products elicits neural activity in areas dedicated to mental state attribution. *Cerebral Cortex, 19,* 619–623. doi:10.1093/cercor/ bhn110

Szego, P. A., & Rutherford, M. D. (2008). Dissociating the perception of speed and the perception of animacy: A functional approach. *Evolution and Human Behavior, 29,* 335–342. doi:10.1016/j.evolhumbehav.2008 .04.002

Thomsen, L., Frankenhuis, W. E., Ingold-Smith, M., & Carey, S. (2011). Big and mighty: Preverbal infants mentally represent social dominance. *Science, 331,* 477–480.

Tiedens, L. Z., & Fragale, A. R. (2003). Power moves: Complementarity in dominant and submissive nonverbal behavior. *Journal of Personality and Social Psychology, 84,* 558–568. doi:10.1037/0022-3514.84.3.558

Tinbergen, N. (1951). *The study of instinct*. Oxford, UK: Oxford University Press.

Trigger, B. G. (1990). Monumental architecture: A thermodynamic explanation of symbolic behaviour. *World Archaeology, 22,* 119–132. doi: 10.1080/00438243.1990.9980135

Trigger, B. G. (1993). *Early civilizations: Ancient Egypt in context*. Cairo, Egypt: American University in Cairo Press.

Van Cappellen, P., & Saroglou, V. (In press). Awe activates religious and spiritual feelings and behavioral intentions. *Psychology of Religion and Spirituality*.

Whitehouse, H. (2004). *Modes of religiosity: A cognitive theory of religious transmission*. Lanham, MD: Rowman & Littlefield.

Wilson, D. S. (2002). *Darwin's cathedral: Evolution, religion and the nature of society*. Chicago, IL: University of Chicago Press.

Wiltermuth, S. S., & Heath, C. (2009). Synchrony and cooperation. *Psychological Science, 20,* 1–5. doi:10.1111/j.1467-9280.2008.02253.x

Zahavi, A. (1975). Mate selection - a selection for a handicap. *Journal of Theoretical Biology, 53,* 205–214. doi:10.1016/0022-5193(75)90111-3

Zanolie, K., van Dantzig, S., Boot, I., Wijnen, J., Schubert, T. W., Giessner, S. R., & Pecher, D. (2012). Mighty metaphors: Behavioral and ERP evidence that power shifts attention on a vertical dimension. *Brain and Cognition, 78,* 50–58. doi:10.1016/j.bandc.2011.10.006

Part III

Chapter 7: Sensory Exploitation And Cultural Transmission: The Late Emergence Of Iconic Representations In Human Evolution

Introduction

In the past, several hypotheses about the evolution of art, including iconic representations (i.e., figurative imagery, realistic art), have been proposed. These hypotheses differ as to whether art is an adaptation or not (e.g., Pinker 1997, 2002), on which level it is selected—the cultural level (Boyd and Richerson 1985, chap 8; 2005) or the genetic level—and which mechanism is responsible for its evolution— mating display (Miller 1998, 1999, 2000, 2001), group bonding (Coe 2003; Dissanayake 1992, 2001), and so on. These different suggestions are all possible solutions to the same problem: the high costs of art production (it is known to be resource, time, and energy consuming). How could such a costly behavior have emerged? Are the costs compensated by benefits (art as an adaptation)? Or are they merely borne by a system that can support a certain amount of suboptimal variants (art as a consequence of non-adaptive evolution)? In order to answer these questions, we need a framework in which all hypotheses about art can be articulated and evaluated. Previously, we have proposed the concept of SE to this end (Verpooten and Nelissen 2010; Chapter 7). In this article, we will first discuss why SE should be considered when modeling the evolution of iconic representations. Then we will apply the concept specifically to shed light on the late emergence of iconic representations in human evolution.

The concept of sensory exploitation

The concept of Sensory exploitation (SE) is based on a model from sexual selection theory of the same name. In sexual selection, SE is a fairly recent model that specifically focuses on female preferences in mate choice. These female preferences result from pre-existing biases of the female psychosensory[17] system that function in other contexts such as finding food or avoiding becoming food. Male display traits evolve to exploit these pre-existing female biases to achieve matings. Some scholars have defended SE as an alternative to indirect benefit models such as Good Genes Selection and Fisher's Runaway Process (e.g., Ryan 1998). Almost all biologists agree today that SE may provide the initial nudge for the evolution of male displays, although they are still debating the relative roles of SE and indirect benefit models in the subsequent evolution and maintenance of female mating preferences and male display traits (Fuller et al. 2005). Some empirical data does seem to indicate that SE is also important in maintaining traits. For instance, when male display traits are obviously mimicking signals as is the case in the egg spots of cichlids. In that case, a runaway process would compromise the success of the mimic. Therefore, SE is a primary force in the evolution of male display traits, and selection through indirect benefits is merely secondary (Kokko et al. 2003).

Arnqvist (2006) usefully distinguishes two main types of sensory biases. First, females are adapted to respond in particular ways to a range of stimuli in order, for example, to successfully find food, avoid becoming food for predators and breed at optimal rates, times, and places. Such multi-dimensional response repertoires form a virtually infinite number of pre-existing sensory biases that are potential targets for novel male traits. Arnqvist (2006) refers to these biases as ''adaptive sensory biases.'' Notice that male traits that result from exploiting these adaptive sensory biases are often ''mimics''.[18]

Secondly, pre-existing sensory biases need not be the direct result of selection. In theory, they can simply be incidental and selectively neutral consequences of how organisms are built (e.g., Endler and Basolo 1998). For example, artificial neural network models have shown that networks trained to recognize certain stimuli seem to generally produce various sensory biases for novel stimuli as a by-product (e.g., Arak and Enquist 1993). Similarly, research in ''receiver psychology" (e.g., Guilford and Dawkins 1991) has also suggested that higher brain processes may incidentally produce pre-existing sensory biases for particular male traits. Following Arak and Enquist (1993), Arnqvist (2006) refers to such sensory biases as

---

[17] The term "psychosensory" is used here as a synonym for "sensory" to stress that we do not only focus on hidden preferences but also on adaptive sensory biases (see further)—which often have a learned and emotional aspect, and a psychological, social and even cultural dimension.
[18] For biologists the term "mimic" usually refers to a whole, mimicking organism (e.g., Pasteur 1982), but Maran (2007, p. 237)—in our opinion usefully—argues from the semioticist view: "...neither the mimic nor the model needs to be a whole organism but can be just a part of an organism both in spatial or temporal terms or just a perceptible feature." Therefore, here we use mimic in the latter sense.

''hidden preferences.'' These, then, can be seen as side-effects or contingencies of how the sensory system, defined in its widest sense, of the receiver is constructed. Usually, it results in abstract biases, for symmetrical or exaggerated traits, for instance (Ryan 1998).

Sexual selection models prove to apply well to the evolution of human artistic and esthetic behavior because of the crucial role perception plays in sexual selection as in art and because both function as intraspecies signaling system. Moreover, there are conspicuous similarities between human artistic behavior and sexually evolved display behaviors in other animals (Darwin 1871)—e.g., bower decoration by male bowerbirds. Miller (1998, 1999, 2000, 2001) applied the indirect benefit model to explain the evolution of art, explicitly excluding a possible role for pre-existing psychosensory biases. We have argued that, based on current findings in sexual selection, he thereby underestimates the explanatory power of SE regarding the evolution of art (Verpooten and Nelissen 2010; Chapter 7). The above-mentioned facts, i.e., that SE provides the initial nudge and a primary force in the evolution of male display traits, equally apply to the evolution of artistic behavior (i.e., producing and experiencing art). It is important to note that, although the concept we use is based upon a model from sexual selection, we do not intend to hypothesize here that art production evolved as a sexually selected trait (nor do we exclude it as a possibility). We only use SE for its mechanism: the interaction between psychosensory biases and traits that evolved by exploiting these biases. In our view, this mechanism can also work in non-sexual contexts; we are only looking at sexual selection as a signaling system analogous to artistic behavior. It is clear from the evidence in sexual selection that the primary force of SE will always be present. The same applies to art. Secondary forces, such as indirect benefits (e.g., as a mating display see Miller 1998, 1999, 2000, 2001), may be operating but are in principle not required for art to evolve. Therefore, here we will explore how far we can get without a priori invoking these secondary processes.

Sensory biases and art

Van Damme (2008, p. 30) describes art as follows: ''Numerous contemporary definitions of the term ''art'' mention in one way or another both ''esthetics'' (denoting say, high quality or captivating visual appearance) and ''meaning'' (referring to some high quality or captivating referential content) as diagnostic features, although any clear-cut distinction between the two appears unwarranted, if only since there is no signified without a signifier.'' This description is very well suited for our evolutionary approach from the SE perspective. The distinction Van Damme makes between esthetics and meaning roughly corresponds to the distinction made by Arnqvist (2006) mentioned above, between hidden preferences influencing the design of signals and adaptive sensory biases influencing the content of signals, resulting in mimicking signals, respectively. Thus, from a broad signal evolution perspective, we can state that what Van Damme has called esthetics, corresponds to design, and results from the exploitation of hidden preferences, and what he has called meaning corresponds to content and results from exploitation of adaptive sensory biases, by mimicking signals or traits.

The role of sensory or perceptual biases in the evolution of art has already extensively been investigated by several researchers (e.g., Hodgson 2006; Kohn and Mithen 1999; Ramachandran and Hirstein 1999). Essentially, they all have focused on the abstract, geometric aspect of visual art. They state that art emerged because its geometric patterns are supernormal stimuli to the neural areas of the early visual cortex. As such (exaggerated) symmetry, contrast, repetition, and so on, in visual art hyperstimulate these early neural areas. Thus, they have focused on what we have called hidden preferences. We agree with these authors that hidden preferences probably play an important role in the design aspects of human visual representations as they do in the design of male display traits. Hodgson (2006) is particularly relevant to our discussion as his focus is also on the emergence of prehistoric art. He has made some observations that are very significant to our proposal (see further).

However, as indicated by Van Damme's definition, design is only one aspect of human visual art—content, or meaning (mimics/iconic representations as the result of adaptive sensory biases) is at least as important in most cases. We will make this clear by way of example in the next section: a comparison between egg spots in cichlids and visual art in humans from a semiotic viewpoint. This is followed by an introduction to some of the human adaptive sensory biases exploitable by iconic representations.

Iconic representations as a result of adaptive sensory biases

Semioticists generally agree that biological mimicry is a semiotic phenomenon (Maran 2007). In his essay, ''Iconicity'' Sebeok (1989) demonstrates that mimicry is a case of iconicity in nature. ''A sign is said to be iconic when the modeling process employed in its creation involves some form of simulation'' (Sebeok and Danesi 2000) and this is exactly what happens when adaptive sensory biases are exploited. We suggest that this also works the other way around: not only are mimics icons, visual art, or more specifically iconic representations (i.e., realistic art, figurative imagery) can be usefully perceived as mimics resulting from exploitation of human adaptive sensory biases.

Van Damme (2008, p. 38) defines iconic representations as: ''The two- or three-dimensional rendering of humans and other animals, or to be more precise, the representation of things resembling those in the external world, or indeed imaginary worlds, fauna and flora especially, but also topographical features, built environments, and other human-made objects.'' This definition is equally applicable to mimics. Many cichlid species independently evolved mouth breeding as a highly specialized brood care behavior. In different lineages of mouth breeding cichlids, we can find egg dummies, formed of various parts of the body, which resemble the ova of the corresponding species. The most abundant form of these is egg spots, which are conspicuously yellow spots on the anal fin of males. Females of mouth breeding cichlids undoubtedly evolved sensory capabilities to detect eggs and are supposed to have a strong affinity for them, as they pick them up immediately after spawning. In fact, the ability to detect the eggs directly affects the female's fertility: Every missed egg results in a reduction in fitness. Consequently, a preexisting sensory bias may have been present in early mouth breeders and may still be present in mouth breeding species which lack egg dummies. As a consequence, males would have evolved egg spots in response to this female adaptive sensory bias. After the female (receiver) has picked up her eggs (model), the male displays in front of her showing the egg spots on his anal fin (mimic). The female responds to the life-like egg illusion with a sucking reaction, and obtains a mouthful of sperm from the canny male in the process. It may be that the female's mating preference for a male with well-elaborated egg spots does not yield any direct benefits for the female nor any good genes for the viability of the female's offspring. Runaway selection is also limited by the mimicking function of the egg spots: they may need to remain life-like to mislead the female. Thus, this may well be an example of the strong version of SE. The female's preference could be solely maintained by the benefit of the detection of eggs after spawning (Tobler 2006) (Fig. 3).

What is interesting for the problem of the evolution of human representational art, is that cases of mimicry like this one show how ordinary selection via SE can produce two-dimensional representations (the egg spots) on a surface (the anal fin of the male) of three-dimensional objects (the eggs). To a female cichlid both the signal from the egg and the signal from the egg spot mean ''egg,'' in the sense that she responds indiscriminately toward both those signals with a sucking reaction. In the same way, humans react toward iconic representations—even though we might ''know'' it is an illusion—as we react to the real thing. However, there is a difference between humans looking at art and the female cichlid looking at the egg spots: she really is deceived, whereas we know we are looking at a painting of a landscape and not at the

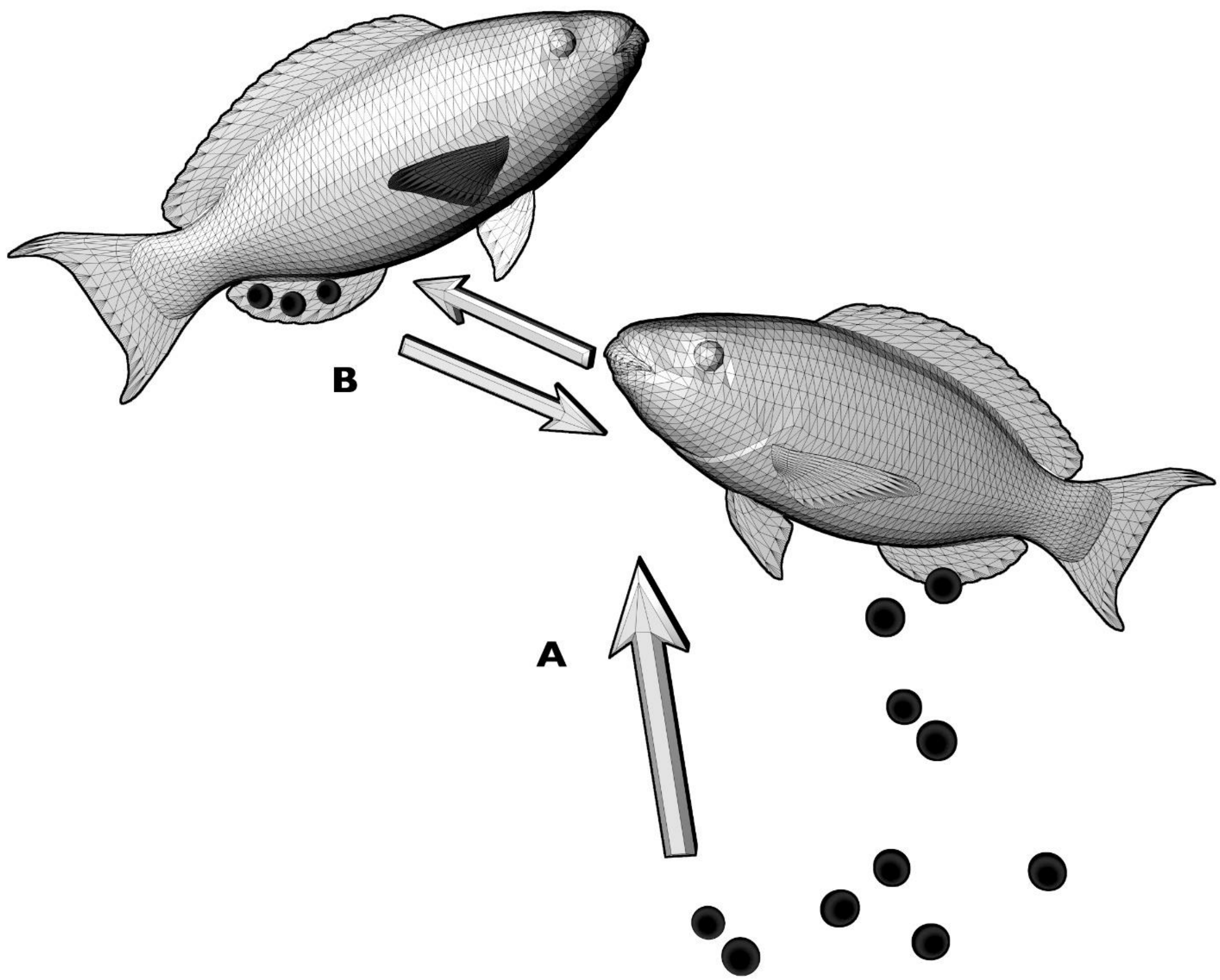

Figure 3. The mating system of mouth breeding cichlids. (A) After laying her eggs the female (right) sucks them up in her mouth. Her ability to detect the eggs is strongly selected for, since every missed egg results in a reduction of fitness. (B) This ability depends on a hair trigger response to ''egg signals.'' Subsequently, males (left) evolved egg spots, accurate two-dimensional mimics the eggs, to exploit this female response. Choice-display coevolution is inhibited by the fact that the female's bias for eggs is vital for detecting the eggs, and there is no reason to a priori state that the effectiveness of the male egg spots are linked to genetic quality. So, this may well be an example of the strong version of sensory exploitation (artwork: Alexandra Crouwers and Jan Verpooten).

real thing. However, does this distinction really matter? Not materially. For even though we know the movie or the novel, for instance, is not real, we still become deeply emotionally involved. Even though we might know it is fiction, we react as if it is not. Art exploits our visual system in the case of iconic representations and our emotions, regardless of our consciousness of the distinction between fiction and reality. Human iconic representations are mimics and as such also result from SE.

One of us (Mark Nelissen) has performed considerable research on cichlids and has described the system of the egg spots (in Tropheus and Simochromis). During courtship, males vibrate their body while showing the egg spots to the female. It could well be that by doing this they enhance the egg illusion, giving it a more three-dimensional effect in combination with the light–dark grading in color and the colorless outer ring the egg spots exhibit. Of course the female reacts toward formal features, design in other words, but this design is not ''just design'' but design designated to evoke meaning.

Rock art researchers throughout the world have explicitly or implicitly invoked ritual as an activity associated with rock art (Ross and Davidson 2006). Just as in the cichlid ritual, here too, the ritual might form an essential part of experiencing the iconic representation, providing an ideal context for deception of the senses. For instance, in the case of cave art, the illusion might have been enhanced by the use of lamps. Cave art must have required artificial illumination both to create it and to view it. The dim, flickering light provided by fat-burning lamps may have been integral to the intended appearance of these subterranean paintings (Debeaune and White 1993). Indeed, it has been suggested by several authors (e.g., Wachtel 1993) that the flickering artificial light created a cinematic effect, in combination with the use of the natural bumpiness of the cave's walls, enhancing the illusion by bringing motion and depth into the depicted animals. In Lascaux, for instance, numerous lamps of this kind have been found (Delporte 1977).

Therefore, instead of focusing on geometrical patterns resulting from exploiting activation of early visual areas of the cortex, we focus on the exploitation of psychosensory or mental biases for iconic images, thus on a higher level of visual processing; for instance, face recognition. Humans have a hair-trigger response to faces. Everywhere we look, we see faces; in cloud formations, in Rorschach inkblots, and so on. The fusiform face area (FFA) is a part of the human visual system which may be specialized for facial recognition (first described by Sergent et al. 1992). It has recently been suggested that non-face objects may have certain features that are weakly triggering the face cells. In the same way, objects like rocky outcroppings and cloud formations may set off face radar if they bear enough resemblance to actual faces (Tsao and Livingstone 2008) (see ''Enhancing accidental iconicity'' section). Whether the hair-trigger response to faces is innate or learned, it represents a critical evolutionary adaptation, one that dwarfs side effects. The information faces convey is so rich, not just regarding another person's identity, but also their mental state, health, and other factors. It is extremely beneficial for the brain to become good at the task of face recognition and not to be very strict in its inclusion criteria. The cost of missing a face is higher than the cost of declaring a non-face to be a face. Therefore, face recognition is an adaptive sensory bias, which is highly susceptible to exploitation by a depiction of a face as a side effect. If our brain had been less sensitive to faces and had stricter inclusion criteria, perhaps many fewer portraits would have been painted throughout art history.

Even though the bias for faces is strong, it is not always exploited. In fact, in many prehistoric iconic representations, the face is not extensively elaborated. This is probably due to the specific context in which the depiction is produced and experienced (analogously, it might be that female cichlids are much less sensitive to ''egg-like signals" a long time after spawning or before spawning). In many representations of the human figure, much more attention is given to specific parts of the body. For instance, in the well-known Upper Paleolithic ''Venus'' figurines, the head is rather schematic, whereas breasts, buttocks, and belly are sculpted in great detail and disproportionately exaggerated. Many different hypotheses have been proposed to explain these distorted female representations (for an overview, see McDermott 1996). While speculative, McDermott's (1996) interpretation is particularly interesting for our approach. He proposes that these disproportions resulted from egocentric or autogenous (self-generated) visual information obtained from a self-viewing perspective. In other words, the disproportions in Venus figurines result from the position of the female creators' eyes relative to their own bodies. Indeed, we shall argue below in ''Enhancing accidental iconicity'' section that self-exploitation of perceptual biases[19] may have been the first step in the emergence of iconic art. Whether these Venus figurines were created as self-representations, as fertility symbols or as erotic items, and whether they were created by men and/or women, they may constitute material evidence of strong adaptive sensory biases for above-mentioned parts of the female body.

We have already touched upon another frequently recurring theme in art history and even more so in art prehistory: the depiction of animals (large wild animals are among the most common themes in cave paintings). Again, a set of adaptive sensory biases might be one of the underlying causes of the tendency to depict animals. In particular, some have speculated that this could well be drawn back to the shared human capacity for ''biophilia'' (Wilson 1984). Biophilia is defined as a biologically based or innate

[19] In this case, the adaptive attention toward vital reproductively functional parts of her own body.

predisposition to attend to, or affiliate with, natural- like elements or processes (Kellert and Wilson 1993). This set of tendencies is claimed to be the result of human evolution in a natural world in which human survival significantly depended on interactions with natural elements and entities, such as animals (animals could be, for example, predator or prey). Leading biophilia theorists have characterized it as including both positive and negative affective states toward natural-like elements.[20] These affective states may be exploitable by artificial natural-like signals, such as iconic representations of natural elements. For instance, the depictions of large cats in Grotte Chauvet (believed to be one of the oldest two-dimensional iconic representations) might have elicited a fear response, drawing attention to the depiction. What art needs to be maintained, improved, and reproduced over different generations, in other words to become a ''tradition'', is to have attention drawn to it.

Is iconic art production genetically and/or culturally transmitted?

In Miller's model, artistic production is maintained by the genetic reproductive success it renders compensating for its costs. In our SE concept, transmission of art production as a human behavior is possible by both genetic and cultural selection, in principle. If visual art is seen as the manifestation of differing sensitivities based upon adaptive sensory biases and hidden preferences, then the persistence of its production can be both the result of genetic level selection and/or cultural level selection. If costs are bearable or if any benefits (cultural or genetic) are involved, persistent psychosensory biases will bias genetic or cultural transmission. The impact of psychosensory biases will depend on several conditions (i.e., costs, benefits, context), but the upper limit is always determined by the costs. The model predicts that the better the costs can be borne, be it by direct benefits or by a greater carrying capacity of the population,[21] the more the psychosensory biases will manifested themselves.

There are some indications from the archeological record that iconic art production is a mainly culturally transmitted behavior, while the ability to experience and interpret art is not and does in fact predate art production, just as the origin of female sensory biases leading to mate preferences sometimes predates exploitation (e.g., Ryan 1998). One of these indications is provided by Hodgson (2006). He remarks that

---

[20] Some also make a distinction between biophilia and biophobia: the former refers to positive, while the latter to negative affective states towards natural-like processes and elements (see Ulrich 1993). This, however, seems largely a terminological discussion. The crux of the matter is that there are some biologically based affective responses to biological categories.

[21] According to Boyd and Richerson (1985, p. 278) each culture may contain a number of afunctional or counterfunctional traits.

the ‘‘first art,’’ both (pre)historical and developmental (children’s first drawings are abstract patterns), is geometric. Therefore, what he calls ‘‘geometric primitives’’ predate iconic art. Hodgson further notices that no culture has ever been shown to have an iconic art tradition without a geometric tradition, but vice versa, some cultures only have a geometric tradition. He draws from this that the making of geometrics may be a more accessible process than the making of representational motifs and that knowledge of geometrics may be innate whereas, we could add, making representations is not and requires individual learning and social transmission of skills to be evolutionary maintained. In the following section, we will explore how social learning could have played a major role indeed in the development of iconic art traditions. This hypothesis is supported by the coincidence between demographic transitions determining social transmission and the emergence of iconic art traditions.

The emergence of full-fledged iconic art traditions

Sensory exploitation may provide the initial nudge for the evolution of visual art as it does in sexual selection (Kokko et al. 2003). However, does it also provide a mechanism that is responsible for the persistence of visual art across cultures? If no indirect benefits are derived—that is, if an adaptive explanation is excluded—the evolution and maintenance of male ornaments may be driven exclusively by SE, the same goes for the evolution and maintenance of artistic production as a behavior. Here, we will investigate this theoretical possibility on the basis of empirical data. This section is primarily based on Powell et al. (2009).

It is only after the Upper Paleolithic transition, which occurred in Europe and western Asia about 45,000 years ago (ka) (Bar- Yosef 2002; Mellars 2005), and later in southern and eastern Asia (James and Petraglia 2005; Petraglia 2007), Australia (Brumm and Moore 2005; O’Connell and Allen 2007), and Africa (Ambrose 1998a) that more complex figurative art appears consistently in the archeological record. This period is seen by many as marking the origins of modern human behavior. Upper Paleolithic material culture, usually referred to as the Late Stone Age in Africa, is characterized by a substantial increase in technological and cultural complexity, including not only the first consistent presence of iconic representations but also other symbolic behavior, such as abstract art and body decoration (e.g., threaded shell beads, teeth, ivory, ostrich egg shells, ocher, and tattoo kits); systematically produced microlithic stone tools; functional and ritual bone, antler, and ivory artifacts; grinding and pounding stone tools; improved hunting and trapping technology; an increase in the long-distance transfer of raw materials; and musical instruments, in the form of bone pipes (Mellars 2005, Bar-Yosef 2002, Brumm and Moore 2005, Ambrose 1998, McBrearty and Brooks 2000).

The oldest evidence of this iconic art traditions appears from around 35 ka on. There are the schematic, monochrome, red paintings on rock fragments from Fumane Cave in northern Italy and the impressive painted depictions of animals from Grotte Chauvet in the Arde`che in southern France (Floss and Rouquerol 2007). Human and animal figurines of approximately this age were found in Stratzing in the Wachau of Lower Austria (Floss and Rouquerol 2007) and in Vogelherd and Hohlen Fells cave, in southwestern Germany (Conard 2003). In the latter, very recently, a Venus figurine was found which was produced at least 35 ka (predating the well-known Venuses from the Gravettian culture by at least 5,000 years) (Conard 2009). The oldest evidence for Middle Stone Age figurative art in Africa is seven paintings on mobile stone blocks from Apollo 11 Cave in southwestern Namibia, which date from between 25.5 and 27.5 ka (Vogelsang 1998).

How could SE help to explain that during the Upper Paleolithic/Late Stone Age iconic representations became widespread, complex, and persistently present across continents and cultures? As we postulated that iconic representations evolved by exploiting pre-existing biases, one could wonder why it did not come to full bloom much earlier. Indeed, it follows that these biases predate the Upper Paleolithic/Late Stone Age extensively.

Until very recently, the appearance of consistent and complex painting and sculpture in the Upper Paleolithic was considered to be part of a more general ‘‘cognitive revolution,’’ with scholars employing such expressions as ‘‘creative explosion’’ (Van Damme 2008). Indeed, some have suggested (Klein 2000; Mithen 1996) that the main cause of behavioral modernity, one of whose hallmarks is considered to be the creation of complex figurative art, was a heritable biological change (mutation(s) with neurocognitive consequences) just before the Upper Paleolithic/Late Stone Age. Meanwhile, many authors have argued that anatomical modern humans possessed the requisite capacities long before the Upper Paleolithic/Late Stone Age (e.g., Mellars 2005, McBrearty and Brooks 2000). It is now widely accepted that anatomical modern humans evolved in Africa some 160–200 ka (e.g., McBrearty and Brooks 2000) (and expanded into most habitable parts of the Old World between 90 and 40 ka; e.g., Ambrose 1998b). The findings mentioned above contradict the theory that a neurocognitive change had to take place to produce Upper Paleolithic/Late Stone Age iconic representations. Moreover, in Africa, the idea of a single transition has been contested (McBrearty and Brooks 2000) because there is strong evidence of the sporadic appearance of many other markers of modern behavior at multiple sites as early as 70–90 ka (Bar-Yosef 2002, McBrearty and Brooks 2000) and possibly as far back as 160 ka (Marean et al. 2007). Therefore, again, how could the delay of some 100,000 years between anatomical modernity and consistent presence of more complex iconic art be explained (Mellars 2005)?

We know how and why egg spots evolved in haplochromines cichlids: they have been proven to be a genetic trait that provides a selective advantage because they encourage females to participate in oral mating (Salzburger et al. 2007). However, as discussed above, the Upper Paleolithic/Late Stone Age transition does not seem to be the result of immediate genetic level changes. Instead, we suggest, as have others (e.g., Shennan 2001; Powell et al. 2009), that it resulted from demographic changes which affected transmission on the cultural level. We propose that Upper Paleolithic/Late Stone Age iconic representations evolved from exploitation of human psychosensory biases via the accumulation of more basic, culturally transmitted ingredients of artistic behavior. The ability to create an iconic representation such as the ones dating some 35 ka requires skills and knowledge which a solitary individual cannot acquire during one lifetime (see further). In other words, Upper Paleolithic/Late Stone Age art requires a cultural tradition, a gradual accumulation of innovations built upon previous ones, maintained by social learning. Without imitation and observation of others, an individual will not acquire the skills and other innovations necessary to produce, for instance, a cave painting like the ones created around 35 ka. True, someone must have been the first to invent a particular relevant skill, but without incorporation into the cultural repertoire via cultural transmission, acquired skills will not be retained, nor be further improved upon over the generations.

Empirical evidence from different research fields suggest the larger the interacting pool of social learners is— i.e., the ‘‘effective population size’’ (Henrich 2004)—the greater the number (and complexity of) cultural innovations in a population (in wild orangutans and chimpanzees: e.g., van Schaik and Knott 2001; in humans: e.g., Henrich 2004). Some data suggest that cultural changes, which could have increased effective population sizes, actually took place around 45 ka. For instance, the flowering of long distant contact (e.g., White 1982), greater tendencies toward colonization (Stiner and Kuhn 2006), and an overall population increase (Bar-Yosef 2002). Which innovations were maintained by cultural transmission—and why they were maintained—are the next questions to be addressed. Three recent cultural evolutionary models (Henrich 2004; Shennan 2001; Powell et al. 2009), which explicitly demonstrate the positive effect of increasing population size on the accumulation of beneficial culturally inherited skills, have been proposed as an integral explanatory component of the appearance of modern behavior. Henrich’s model

(2004) demonstrates that under certain critical conditions, directly biased transmission can lead to cumulative adaptation of a culturally inherited skill. He terms this as ‘‘cumulative adaptive evolution” which depends on a critical population size.

Powell et al. (2009) adapt and extend Henrich's transmission model (2004) into a more realistic structured metapopulation, which reflects plausible late Pleistocene conditions, to investigate the effects of demographic factors on the accumulation (or loss) of cultural complexity. The results of their simulation demonstrate that the influence of demography on cultural transmission processes provides a mechanism to explain, among other things, the delay between the emergence of anatomical modern humans as a species and the material expression of modern behavioral traits.

A problem, however, with these models with respect to the subject at hand—i.e., iconic representations, is their basic assumption of adaptiveness. Increased complexity of skills is associated with increased adaptiveness. This is true for technological utilitarian skills, and perhaps also for the creation of symbols that function in identifying groups (i.e., ethnic markers) (Boyd and Richerson 2005), but not necessarily for iconic representations, which may not have a utilitarian purpose at all, nor a function in evolutionary terms. At certain times and places throughout human evolution, producing and experiencing iconic representations may have been neutral or even maladaptive, depending on specific conditions. The question as to whether visual art such as iconic representations is, or has been, adaptive or not is thus a tricky one, and hard to answer. Illustrative of this are the divided opinions on adaptiveness of visual art (e.g., Pinker 2002). Moreover, under the proponents of art as adaptive there is no consensus in what way it actually would be. To some, it is sexually adaptive (e.g., Miller 1998, 1999, 2000, 2001), to others, it is a group adaptation (Coe 2003; Dissanayake 1992, 2001). We conclude that if it can be shown that iconic representations evolve even when they are maladaptive, they definitely will when they induce some kind of benefits on any kind of unit of selection. Therefore, here we propose a model in which iconic art tradition can evolve without any adaptiveness assumptions as a mere consequence of SE and demographic changes.

An iconic art tradition could only have evolved as a consequence of the accumulation of several innovations in artistic production behavior, whereby more complex ones are built upon simpler ones. For instance, rock artists needed to know where to find pigments and how to process them for use. Also, possibly, knowledge of locations with usable surfaces for painting needed to be maintained in the collective memory of the population by cultural transmission. Secondly, innovations concerning painting skills and methods needed to accumulate. These include intensive training in hand skills or fine motor skills for drawing and insight into how a real object can be translated into a twodimensional representation that suggests three-dimensionality through shading and skillful use of colors (e.g., the rock art in Grotte Chauvet). Naturally, some of these innovations also function in other contexts, such as trained fine motor control in tool making and use and pigments in ceremonial or ritual contexts (Power 1999). We probably need to distinguish two categories of innovative or cumulated skills: the ones that are retained solely for the purpose of iconic art production (e.g., drawing skills); and the ones that are primarily retained for other, utilitarian, purposes. We expect that some of the complex skills resulting from Henrich's (2004) ''cumulative adaptive evolution'' would enable, as a side-effect to their effectiveness in technological practices, exploitation of psychosensory biases through the production of iconic representations.

Thus, demographic transition enabled evolution of iconic art traditions through increased capacity to maintain innovations of art production. Even if the resulting iconic art tradition is not adaptive, the general adaptiveness of the populations of social learners increased in the Upper Paleolithic/Late Stone Age which made its capacity higher. This allowed for neutral and even maladaptive practices to evolve as a result of SE, instead of being eliminated by natural selection (Fig. 4).

Enhancing accidental iconicity

However, didn't SE leave any marks of its working from before the Upper Paleolithic/Late Stone Age transition? It seems there are some findings, albeit sparse and controversial, of collecting stones and protosculptural activity that seem to fit SE particularly well. The findings we refer are to predate the appearance of a consistent iconic tradition. They point to the collection and enhancement of stone objects that are accidentally iconic—i.e., they coincidentally attract the attention of humans by playing upon their adaptive sensory biases.

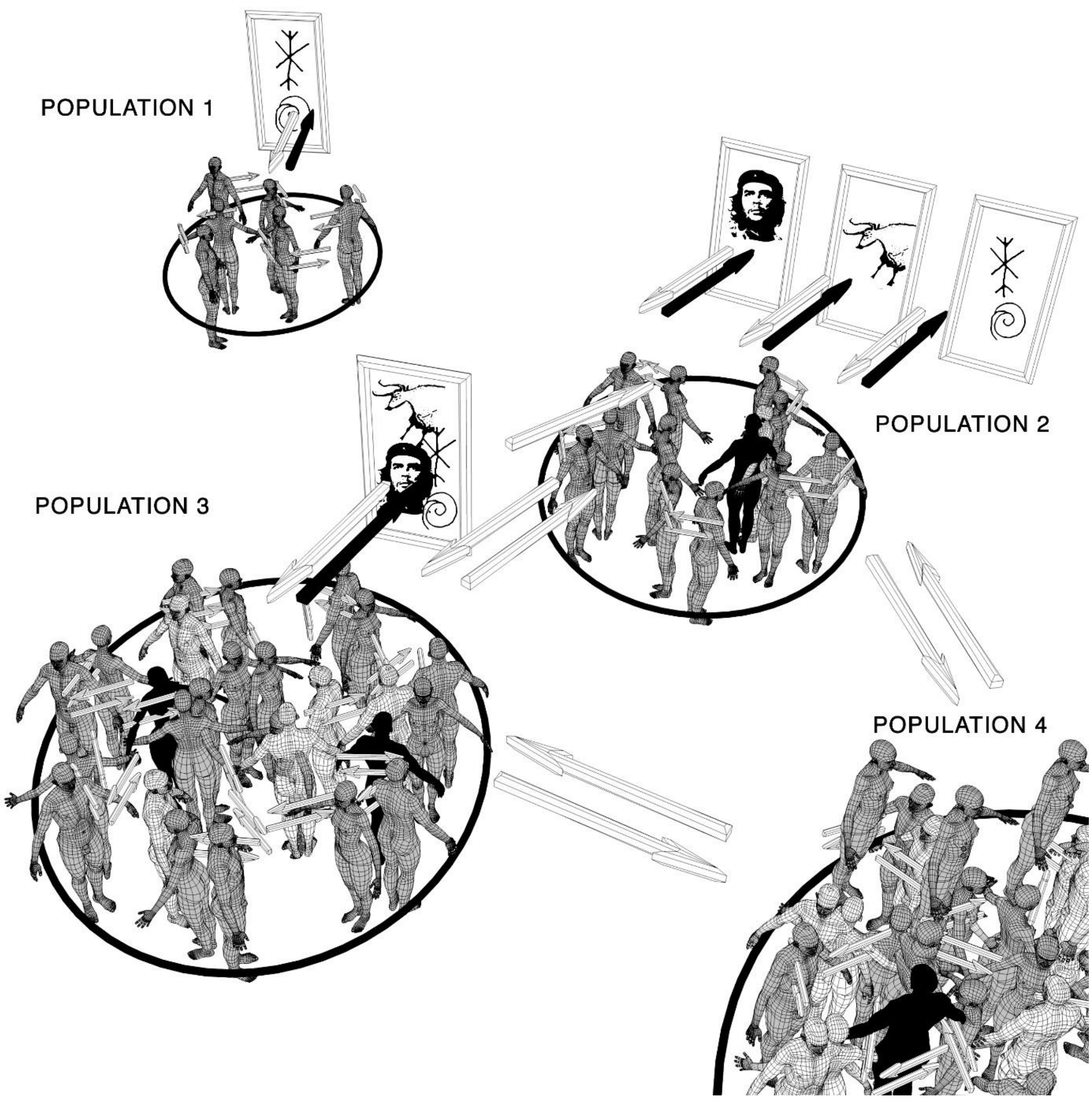

Figure 4. Sensory exploitation, cultural transmission and the influence of the size of the interacting pool of social learners on art. In this figure four hypothetical populations of social learners and the artworks that they produce are shown. All arrows stand for the direction in which ''information''is transmitted. In addition, when the arrow is black, that information directly determines the outward appearance of an artwork. This kind of information will come from the artist that created the work, which are also represented in black. Driven by the process of sensory exploitation, artists will create artworks that exploit theirs and others' pre-existing biases. Portraits result from exploitation of biases caused by face recognition and animal depictions from biases caused by biophilia (or biophobia). Population 1 is a small and isolated population of social learners. As a result, the innovations required for its members to produce iconic art will not accumulate. They will however produce abstract art that does not require (much) social learning (Hodgson 2006). In populations 2–4 iconic art traditions will naturally and necessarily occur because these are large and interconnected, creating an interacting pool of social learners that is large enough for innovations required for

production iconic art to spontaneously accumulate and persist regardless any beneficial effects of the artworks (artwork: Alexandra Crouwers and Jan Verpooten).

The most recent finding is a large piece of rock—6 m long and 2 m high—found in a cave in the Tsodilo Hills in Botswana and resembling the body and head of a python (press reports, late 2006). The surface of the rock shows hundreds of artificial indentations that might have been applied to suggest a snake's scales. The indentations appear to have been made by stone tools excavated in the cave and are provisionally dated to more than 70 ka.

Two modified stone objects date further back in time. The so-called Tan Tan figurine found in Morocco is a small stone whose natural shape resembles that of a human being. Some of the object's natural grooves, which are in part responsible for its anthropomorphic appearance, seem to have been accentuated artificially in what is interpreted as an attempt to enhance the human resemblance. It has been provisionally dated to between 500 and 300 ka (Bednarik 2003). The ''Berekhat Ram figurine,'' Israel, is dated 233 ka and presents a similar case of semi- or protosculptural activity (Goren-Inbar 1986). The oldest object found at a hominid occupation site is a naturally weathered pebble resembling a hominid face, without any of these anthropogenic enhancements. The site in Makapansgat, South Africa, where it was found is dated 3 million years old (Dart 1974).

Even though they are sparse and controversial, it is significant for the application of the concept of SE to Paleolithic art that all these early findings appear to be (enhanced) semblances. Concerning paintings, we mentioned earlier that the natural bumpiness of a rocky surface is often used to enhance the three-dimensionality of depictions. In fact, some of the paintings on natural bumps may have been created as enhanced semblances. From the SE perspective, one would expect that the first iconic representations originated from accidental exploitation by natural objects that elicit responses. Imagine an early human stumbling upon a stone that draws her attention because it triggers a strong response as a result of adaptive sensory biases, exhibiting ''accidental iconicity.'' If it resembles a human face it could play upon the FFA. She might keep the stone, start a collection of objects that draw the attention of her adaptive sensory biases. Later, she might even start scratching at it with a harder stone, deepening its natural crevices, resulting in something that looks even more like a face. She acts probably driven by her own responses to the ever enhancing ''mimic'' of a human face. This specific case (an initial spark of artistic behavior) would be an incident of self-exploitation. Logically, the first person upon which the ''effectiveness'' of an artwork is tested is the artist herself. Not only when ''finished'' but also during the several intermediate stages in the artistic process. When (the products of) these self-exploiting behaviors subsequently become part of a socially transmitted cultural repertoire they evolve into traditions by the accumulation of innovative variants, as discussed in the previous section.

One might object that the analogy between biological signal evolution through SE and the evolution of human art behavior ends when considering self-exploitation. However, male fiddler crabs prove otherwise. Courting male fiddler crabs sometimes build mounds of sand, called hoods, at the entrances to their burrows. Males wave their single enlarged claws to attract females to their burrows for mating. It has been shown that burrows with hoods are more attractive to females and that females visually orient to these structures. Interestingly, a recent study showed that males themselves were also attracted toward their own hoods as a consequence of SE or sensory trap (Ribeiro et al. 2006). Hence, hood building, like art production, causes self-exploitation.

Another objection one could make is that in the anecdote of the early artist the artistic process through sensory (self-)exploitation occurs on the individual level, while SE as an evolutionary selection process typically occurs on the population level—evolution is a change in gene frequencies in a population that usually occurs over many generations. For instance, mound building in male fiddlers probably evolved gradually because of the increased reproductive success SE of females yielded for the mound builders relative to the non-mound builders. Probably because males and females share a lot of the same sensory biases and responses, the males are equally attracted to their own mounds. Therefore, mound building evolves on the evolutionary level—that is, through sexual selection, over many generations.

However, one should not exaggerate this distinction between the crab and the artist. First, the artistic process described here in an anecdotal form may in fact occur far more gradually and also spread over many generations of social learners as we proposed above.

Secondly, in mimicry and SE in other animals, previous experience and learning of the individual plays an important role as well (e.g., ten Cate and Rowe 2007). Also, male bowerbirds when decorating their bowers are reported to inspect their bowers from a distance during the process, like a painter who steps back from his canvas to check the intermediate result while painting.

Moreover, when individual learning has a social component, the cultural transmission of traits influencing behavior is enabled, and cultural transmission has an evolutionary dynamic analogous to genetic transmission, but could occur at a much higher rate, as transmission through social learning can happen all the time (Richerson and Boyd 2001). For instance, in bowerbirds, styles in bower decoration are said to spread over populations and even jump to other species of bowerbirds, via cultural transmission (http://www.life.umd.edu/biology/borgialab/).

Also, stone play in Japanese macaques is a well-documented example of animal behavior that seems to have much in common with human artistic behavior from our viewpoint. Just as artistic behavior, stone play exhibits inventive variations transmitted in a context of social facilitation and observational learning, it does not seem to have any instrumental function and it probably involves some form of self-exploitation (Huffman and Quiatt 1986).

We do not intend to dismiss the idea that certain capacities used in the production of iconic representations are unique to modern humans, but our approach shows that these differences are gradual rather than absolute. As said, biological mimicry illustrates that icons are not only produced in the human species (Maran 2007), we only produce more of them and a greater variety.

Modern culture

The process of the gradual accumulation of the innovative skills and knowledge that affect artistic production, as mentioned above, may have led to something that we might not perceive of as art today, but that nevertheless plays upon a whole range of psychosensory biases, namely multimedia products like movies, advertisement, and video games. These products of modern culture probably have more in common with cave art than cave art has with modern painting. As Marshall McLuhan said: ‘‘Ads are the cave art of the twentieth century.” While these products are directed at exploiting emotional and visual sensitivities, modern art often is not. Its aim is instead conceptual, analyzing and ‘‘deconstructing’’ its own underlying mechanisms. This distinction between modern art and rock art is one of the reasons the use of the term ‘‘art’’ is tricky in a scientific approach. However, as we have hoped to show, a bio-evolutionary account of art such as iconic representations is necessary and worthwhile as it provides a framework in which ideas about more specific aspects of visualizations can be articulated.

Conclusion

We have proposed that the concept of SE combined with ideas about cultural transmission sheds light on the late emergence of iconic art traditions in human evolution during the Upper Paleolithic/Late Stone Age. Scholars disagree on the adaptiveness of art. We have advanced a view in which art can evolve even if it is not adaptive. First, a demographic transition increased the capacity of Upper Paleolithic/Late Stone

Age cultures, enabling an increased tolerance for neutral and even maladaptive traits. Secondly, the same demographic transition led to ''cumulative adaptive evolution'' and as such to more complex adaptive skills. Subsequently, these skills could serve potential non-adaptive purposes as well, such as iconic art production. The evolution then of art production is solely driven by SE and not hindered by costs (i.e., elimination by natural selection) because of the high adaptiveness of cumulative culture itself. As such, indirect benefits of iconic art production are not a prerequisite; however, if present, they may additionally drive its evolution as a secondary force. Whether investigated from a biological, sociological, anthropological, or philosophical perspective, one cannot ignore the fact that iconic art draws upon sensory sensitivities. Our view based on SE could serve as a concept that enables articulation and evaluation of all existing hypotheses about art.

Acknowledgements

We thank one anonymous referee, Johan Braeckman and his research group, Andreas de Block, Tijs Goldschmidt, Yannick Joye, and Alexander Verpoorte for sharing useful suggestions and commenting on earlier drafts. Also many thanks to Lokaal01_Antwerpen (www.lokaal01.org) for the opportunity to discuss our ideas among scientists and artists. Last but not least we thank Nathalie Gontier and the other members of the organizing committee for having us at the conference.

References

Ambrose SH (1998a) Chronology of the Later Stone Age and food production in East Africa. J Archaeol Sci 25:377–392 Ambrose SH (1998b) Late Pleistocene human population bottlenecks, volcanic winter, and differentiation of modern humans. J Hum Evol 34:623–651

Arak A, Enquist M (1993) Hidden preferences and the evolution of signals. Phil Trans R Soc B 340:207–213

Arnqvist G (2006) Sensory exploitation and sexual conflict. Phil Trans R Soc B 361:375–386. doi:10.1098/rstb.2005.1790

Bar-Yosef O (2002) The Upper Paleolithic revolution. Annu Rev Anthropol 31:363–393

Bednarik RG (2003) A figurine from the African Acheulian. Curr Anthropol 44(3):405–413

Boyd R, Richerson PJ (1985) Culture and the evolutionary process. The University of Chicago Press, Chicago

Boyd R, Richerson PJ (2005) The origin and evolution of cultures. The University of Chicago Press, Chicago

Brumm A, Moore MW (2005) Symbolic revolutions and the Australian archaeological record. Camb Archaeol J 15:157– 175. doi:10.1017/S0959774305000089

Coe K (2003) The ancestress hypothesis: visual art as adaptation. Rutgers University Press, New Brunswick

Conard NJ (2003) Palaeolithic ivory sculptures from South-Western Germany and the origins of figurative art. Nature 426:830–832

Conard NJ (2009) A female figurine from the basal Aurignacian of Hohle Fels Cave in southwestern Germany. Nature 459:248– 252. doi:10.1038/nature07995

Dart RA (1974) The waterworn pebble of many faces from Makapansgat. S Afr J Sci 70:167–169

Darwin C (1871) The descent of man, and selection in relation to sex, 2 vols. John Murray, London (Reprinted in 1952 by Encyclopedia Britannica)

Debeaune SA, White R (1993) Ice-age lamps. Sci Am 268:108–113

Delporte H (1977) Paleolithic lamp found at cave-of-Lascaux. Rev Louvre mus Fr 27:94–96

Dissanayake E (1992) Homo sestheticus. Where art comes from and why. University of Washington Press, Seattle

Dissanayake E (2001) Birth of the arts. Nat Hist 109:84–91

Endler JA, Basolo AL (1998) Sensory ecology, receiver biases and sexual selection. Trends Ecol Evol 13:415–420

Floss H, Rouquerol N (2007) Les Chemins de l'Art Aurignacien en Europe/Das Aurignacien und die Anfa¨nge der Kunst in Europa. E´

ditions Muse´e-forum Aurignac, Aurignac

Fuller RC, Houle D, Travis J (2005) Sensory bias as an explanation for the evolution of mate preferences. Am Nat 166:437–446

Goren-Inbar N (1986) A figurine from the Acheulean site of Berekhat Ram. J Isr Prehist Soc 19:7–12

Guilford T, Dawkins MS (1991) Receiver psychology and the evolution of animal signals. Anim Behav 42:1–14

Henrich J (2004) Demography and cultural evolution: how adaptive cultural processes can produce maladaptive losses—the Tasmanian case. Am Antiq 69:197–214

Hodgson D (2006) Understanding the origins of Paleoart: the neurovisual resonance theory and brain functioning. Paleoanthropology 2006:54–67

Huffman MA, Quiatt D (1986) Stone handling by Japanese macaques (Macaca fuscata): implications for tool use of stone. Primates 27:413–423

James HVA, Petraglia MD (2005) Interpreting conflict in the ancient Andes. Curr Anthropol 46(Suppl):3. doi:10.1086/425660

Kellert SR, Wilson EO (1993) The biophilia hypothesis. Island Press, Washington

Klein R (2000) Archaeology and the evolution of human behavior. Evol Anthropol 9:17–36

Kohn M, Mithen S (1999) Handaxes: products of sexual selection? Antiquity 73:518–526

Kokko H, Brooks R, Jennions MD, Morley J (2003) The evolution of mate choice and mating biases. Proc R Soc Lond B 270:653–664

Maran T (2007) Semiotic interpretations of biological mimicry. Semiotica 167:223–248. doi:10.1515/SEM.2007.077

Marean CW et al (2007) Early human use of marine resources and pigment in South Africa during the Middle Pleistocene. Nature 449:905–908. doi:10.1038/nature06204

McBrearty S, Brooks AS (2000) The revolution that wasn't: a new interpretation of the origin of modern human behavior. J Hum Evol 39:453–563

McDermott L (1996) Self-representation in upper paleolithic female figurines. Curr Anthropol 37:227–275

Mellars P (2005) The impossible coincidence. A single-species model for the origins of modern human behavior in Europe. Evol Anthropol 14:12–27

Miller GF (1998) How mate choice shaped human nature: a review of sexual selection and human evolution. In: Crawford C, Krebs D (eds) Handbook of evolutionary psychology: ideas, issues, and applications. Lawrence Erlbaum, Mahwah, pp 87–129

Miller GF (1999) Sexual selection for cultural displays. In: Dunbar R,

Knight C, Power C (eds) The evolution of culture. Edinburgh University Press, Edinburgh, pp 71–91

Miller GF (2000) The mating mind. Heinemann, London

Miller GF (2001) Aesthetic fitness: how sexual selection shaped artistic virtuosity as a fitness indicator and aesthetic preferences as mate choice criteria. Bull Psychol Arts 2(1):20–25

Mithen SJ (1996) The prehistory of the mind: a search for the origins of art, religion, and science. Thames and Hudson, London

O'Connell JF, Allen J (2007) Pre-LGM Sahul (Pleistocene Australia- New Guinea) and the archaeology of early modern humans. In:

Mellars P, Boyle K, Bar-Yosef O, Stringer C (eds) Rethinking the human revolution. McDonald Institute for Archaeological Research, University of Cambridge, Cambridge, pp 395–410

Pasteur G (1982) A classificatory review of mimicry systems. Annu Rev Ecol Syst 13:169–199

Petraglia MD (2007) Mind the gap: factoring the Arabian Peninsula and the Indian subcontinent into out of Africa models. In:

Mellars P, Boyle K, Bar-Yosef O, Stringer C (eds) Rethinking the human revolution. McDonald Institute for Archaeological Research, University of Cambridge, Cambridge, pp 383–394

Pinker S (1997) How the mind works. Norton, New York

Pinker S (2002) The blank slate. The modern denial of human nature. Viking, New York

Powell A, Shennan S, Thomas MG (2009) Late pleistocene demography and the appearance of modern human behavior. Science 324:1298–1301. doi:10.1126/science.1170165

Power C (1999) 'Beauty' magic: the origins of art. In: Dunbar R,

Knight C, Power C (eds) The evolution of culture. Edinburgh University Press, Edinburgh, pp 71–91

Ramachandran VS, Hirstein W (1999) The science of art: a neurological theory of aesthetic experience. J Conscious Stud 6:15–51

Ribeiro PD, Christy JH, Rissanen RJ, Kim TW (2006) Males are attracted by their own courtship signals. Behav Ecol Sociobiol 61: 81–89

Richerson PJ, Boyd R (2001) Built for speed, not for comfort. Darwinian theory and human culture. Hist Philos Life Sci 23: 425–465

Ross J, Davidson I (2006) Rock art and ritual: an archaeological analysis of rock art in arid central Australia. J Archaeol Method Theory 13:305–341. doi:10.1007/s10816-006-9021-1

Ryan MJ (1998) Sexual selection, receiver biases, and the evolution of sex differences. Science 281:1999–2003 (review 1999)

Salzburger W, Braasch I, Meyer A(2007) Adaptive sequence evolution in a color gene involved in the formation of the characteristic eggdummies of male haplochromine cichlid fishes. BMC Biol 5:51

Sebeok TA (1989) Iconicity. In: Sebeok TA (ed) The sign and its masters. University Press of America, Lanham, pp 107–127

Sebeok TA, Danesi M (2000) The forms of meaning: modeling systems theory and semiotic analysis. Mouton de Gruyter, Berlin, New York

Sergent J, Ohta S, MacDonald B (1992) Functional neuroanatomy of face and object processing. A positron emission tomography study. Brain 115:15–36

Shennan S (2001) Demography and cultural innovation: a model and its implication for the emergence of modern human culture. Camb Archeol J 11:5–16

Stiner MC, Kuhn SL (2006) Changes in the 'Connectedness' and resilience of Paleolithic societies in Mediterranean ecosystems. Hum Ecol 34:693–712

Ten Cate C, Rowe C (2007) Biases in signal evolution: learning makes a difference. Trends Ecol Evol 22:380–387. doi:10.1016/j.tree. 2007.03.006

Tobler M (2006) Die Eiflecken bei Cichliden: Evolution durch Nutzung der Sinne? (The egg spots of cichlids: evolution through sensory exploitation?) Z Fisch 8:39–46

Tsao DY, Livingstone MS (2008) Mechanisms of face perception. Annu Rev Neurosci 31:411–437. doi:10.1146/annurev.neuro.30. 051606.094238

Ulrich RS (1993) Biophilia, biophobia, and natural landscapes. In: Kellert RS, Wilson EO (eds) The biophilia hypothesis. Island Press, Washington, pp 73–137

Van Damme W (2008) Introducing world art studies. In: Van Damme W, Zijlmans K (eds) World art studies: exploring concepts and approaches. Valiz, Amsterdam, pp 23–61

van Schaik CP, Knott CD (2001) Geographic variation in tool use on Neesia fruits in orangutans. Am J Phys Anthropol 114:331–342

Verpooten J, Nelissen M (2012) Sensory exploitation: underestimated in the evolution of art as once in sexual selection? In: Plaisance KS, Reydon TAC (eds) Philosophy of behavioral biology, volume: Boston studies in the philosophy of science. Springer

Vogelsang R (1998) Middle-Stone-Age-Fundstellen in Su¨dwest- Namibia. Heinrich Barth Institut, Ko¨ln

Wachtel E (1993) The first picture show: cinematic aspects of cave art. Leonardo 26:135–140

White R (1982) Rethinking the middle/upper paleolithic transition (and comments and replies). Curr Anthropol 23:169–192

Wilson EO (1984) Biophilia. Harvard University Press, Cambridge

Chapter 8: Prestige Bias Trumps Content Bias Among Art Experts But Not Among Laypersons

Introduction

Across cultures, people's art preferences tend to gravitate toward particular types of representations: aesthetically pleasing landscapes, animals, and humans (Dutton, 2009). For example, "academic art" is generally preferred and typically depicts beautiful people in lush landscapes (De Smedt & De Cruz, 2012). According to Evolutionary Aesthetics, beauty experiences, evoked by particular elements of the human environment, are unconsciously realized avenues to high fitness in human evolutionary history (Thornhill, 2003). Correspondingly, evidence suggests that aesthetic preferences for certain landscape types, animals, and human appearances may have evolved to guide, respectively, habitat choice, hunting and predator avoidance and peer and mate choice (Barrett, 2005; Falk & Balling 2010; Little, Jones, & DeBruine, 2011; New, Cosmides, & Tooby, 2007; Orians & Heerwagen 1992; Windhager et al., 2011; Yang et al., 2012). However, when such beauty experiences are elicited by artwork, the preference's proper function is probably not preserved - obviously, one cannot mate with a portrait or seek refuge and find food in a painted landscape. Therefore, art may have rather evolved as a nonfunctional byproduct of these preferences. In this sense, art may be a culturally evolved pleasure technology, much like videogames, drugs, or pornography, which are also thought to succeed by exploiting people's otherwise adaptive preferences and motivational systems (Pinker, 1997, 2007). We refer to this account as the byproduct hypothesis.

Indulging in pleasure technologies may be costly for individuals because it consumes valuable time while conveying little meaningful information (Miller, 2006). Moreover, it has been suggested that such culturally evolved technologies may be the culprit behind the paradoxical dissociation between wealth and reproductive success across societies. Indeed, individuals may trade-off rewards from pleasure technologies and biological activities, resulting in less effort being allocated to reproduction (Enquist et al., 2002). However, given their negative effect on biological fitness, countermeasures to highly attractive, persuasive stimuli, such as aesthetically pleasing visual art, may have evolved in humans (cf. Johnstone, 2002). Recent developments in art history seem to support this contention. Note that the byproduct hypothesis predicts that humans would invariably prefer works of art that maximally conform to evolved aesthetic preferences. However, Danto (2003) reports that aesthetic appeal began to lose its central position in contemporary Western art since the beginning of the 20th century, as illustrated by the famous example of Duchamp's Fountain (an ordinary urinal placed in an art exhibition context) of 1917, and he notes that by the 1960s, the idea of beauty had virtually disappeared from contemporary (high) art. Here, we hypothesize that such art-historical developments are due to socially learned art expertise (i.e., an emerging tradition) that is aimed at resisting exploitation by content appealing to evolved aesthetic preferences. Theoretical and empirical work in the field of cultural evolution (a.k.a. dual inheritance or gene-culture coevolution) has shown that the most efficient strategy to acquire better than average expertise in a given domain is to copy the cultural repertoire of prestigious individuals in that domain (Boyd & Richerson, 1985; Henrich & Broesch, 2011; Henrich & Gil-White, 2001). Moreover, research has shown that this prestige bias strategy may override content biases (Henrich & Boyd, 2002). Thus, applying this prestige bias hypothesis to the art domain, we assert that insiders of the art domain (i.e., experts) have learned to avoid exploitation by copying the cultural expertise (which is expressed in artwork and corresponding preferences) of prestigious individuals in the art domain. The greater exposure to art that art experts (i.e., artists, art critics, dealers, etc.) experience should further reinforce their need for resistance against beautiful but costly art. By contrast, the lower exposure to art that outsiders of the art domain (i.e., laypersons, the general audience) experience gives them fewer incentives to learn how to resist exploitation and hence leaves them more vulnerable to exploitation (Johnstone, 2002; Martens & Tracy, 2013). As a nonhuman example, it is illustrative that only naïve male insects are exploited by orchids mimicking females and that they gradually learn how to avoid this exploitation (Wong, Salzmann & Schiestl, 2004; Wong & Schiestl, 2002). Based on this information, we expect that laypersons will neither resist exploitation nor use prestige bias to counter it.

Hence, we predict that expertise moderates the content and prestige effects on art appreciation, such that laypersons' appreciation will be content-biased while experts' appreciation will be prestige-biased. The content effect will be mediated by aesthetic pleasure (Pinker, 1997, 2007), while the prestige effect will be mediated by admiration for the artist (Henrich & Gil-White, 2001).

The present research

To test the byproduct hypothesis, stimuli with aesthetically pleasing content that clearly corresponded to an evolved preference were required. A large body of empirical research suggests that facial attractiveness satisfies this condition. First, perceiving facial attractiveness may elicit aesthetic pleasure, as it is associated with activation of reward- and emotion-related brain areas such as the orbitofrontal cortex, basal ganglia, and amygdala (Kampe et al., 2001; Nakamura et al., 1998; Winston et al., 2007). Second, the rewarding effect of perceiving facial beauty likely serves an ultimate function as it may indicate conspecifics' fitness, and as such, the preference for facial beauty optimizes mate and social partner choices (Little, Jones, & DeBruine, 2011).

To test the hypothesis that among experts, prestige bias would trump the content effect of depicted facial beauty (Henrich & Boyd, 2002), we needed a reliable indicator of prestige. As prestige levels of artwork, artists, and art institutions are inextricably intertwined (de Nooy, 2002), we expected that a prestigious museum context in which the artwork was embedded would act as a proxy of prestige of the artist and the artwork. In addition, because it has been asserted that prestige bias is associated with social emotions such as admiration for the prestigious individual (Henrich & Gil-White, 2001), we assessed this as well.

Study 1 was an exploratory lab study verifying the effects of content and prestige on art appreciation of participants who varied somewhat in expertise. In study 2, also in the lab, we additionally assessed the hypothesized mediating variables, that is, aesthetic pleasure and admiration for the artist, among similar participants. Study 3 replicated the methods of study 2, but we recruited real art experts in addition to laypersons who completed the study online.

Stimuli and manipulations

We used a stimulus set consisting of color portraits that were produced for face research purposes rather than real artwork to avoid effects of familiarity (Schacht, Werheid, & Sommer, 2008). Conveniently, these portraits were taken under identical studio conditions, and they were standardized with respect to frontal view and frontal gaze direction, resolution (300 dpi), and lighting. Accessories (e.g., jewelry or hair clips) were avoided, makeup was restricted to eyeliner, and no clothes were in view. Faces had a neutral expression to avoid effects of affect. The original portraits were reframed to ensure identical display windows and were placed in front of a standardized light gray background (Schacht, Werheid, & Sommer, 2008). As such, important to our purposes, there was no variation between the stimuli with respect to potentially artistically relevant features such as composition, choice of background, technique or even skillfulness (they were all taken by the same photographer). Additionally, the faces had already been rated on attractiveness. To keep it simple, we only used female faces that had received intermediate (control) vs. high ratings of attractiveness. We started off with six portraits in each condition in study 1; however, because appreciation turned out to be highly consistent within conditions (i.e., Cronbach's alphas for each condition were .92), we reduced the number of stimuli to two in each condition in studies 2 and 3 (see Fig. 5). In all three studies, facial attractiveness (i.e., intermediate vs. attractive faces) of the portraits was manipulated *within* subjects.

In all three studies, we manipulated prestige (i.e., neutral vs. the influential Museum of Modern Art or "MoMA") *between* subjects to conceal the fact that we were assessing its effect. Hence, participants were randomly assigned to either one of these conditions; those in the neutral condition were merely told in the introduction screen that they were going to judge artwork, while those in the prestige condition were told in the introduction screen that the artwork they were going to judge belonged to the permanent collection of the MoMA. Anticipating the possibility that a participant did not know the MoMA, the introduction gave some background information about the MoMA, i.e., that it is located in New York and that it is one of the most prestigious museums for modern and contemporary art in the world. To conceal the fact that the stimuli were not real works of art, let alone that they did not belong to the MoMA collection, we used an equal number of "fillers", i.e., artistic portraits that were not used in the analysis but that *were* part of MoMA's permanent collection and that looked somewhat similar to the stimuli (see Electronic Supplementary Materials 2, available on the journal's Web site at www.ehbonline.org). The fillers also served to make the content manipulation (i.e., variation in facial attractiveness of portraits) less apparent.

Figure 5. Stimuli depicting faces previously rated as attractive (left) and moderately attractive (right) (Schacht, Werheid, & Sommer, 2008).

Methods of studies 1 and 2

Participants

One hundred and fifty-two undergraduate students from a large European University participated in exchange for course credits or a participation fee in study 1. One participant who did not finish the survey was excluded from the analysis. The resulting 151 participants ranged in age from 17 to 26 years (*M*= 19.24, *SD*=1.66); 74 were male and 77 female. In study 2, 120 students participated in exchange for course credits or a participation fee. They ranged in age from 18 to 26 (*M*=19.56, *SD*=1.709); 82 of them were male, 38 were female.

Procedure and measures

Participants came to the laboratory in groups of up to 10 persons and were assigned a seat in a partially enclosed cubicle where they completed the study in private on a personal computer. By clicking on an icon, they started the survey, which was created in Qualtrics and which consisted of several blocks in fixed order: an introduction, the pictures, an expertise questionnaire and finally some questions regarding demographics. In the introduction screen, participants were informed about the procedures of the study and the fact that their participation was anonymous and voluntary. They agreed to participate by pressing on the “proceed” arrow.

After the introduction screen, a first picture appeared. In the MoMA condition, the picture said “© MoMA” right below the right corner of the picture; in contrast, in the neutral condition, the picture was not accompanied by such text. Below each picture were statements. In study 1, it was stated “I appreciate this artwork…” followed by a seven-point Likert scale ranging from “not at all ”(=1) to “very much”(=7). In study 2, it was additionally stated, “I find what is depicted aesthetically pleasing…” and “I admire the artist who made this work…,” both followed by the same Likert scales. Only after the participant had completed all statements could she move on to the next picture with statements, and so on. The order of the pictures was randomized and included both the stimuli and fillers.

Subsequently, (subjective) art expertise was probed in both studies 1 and 2 using a questionnaire that we slightly modified for the present studies (Leder et al. 2010). It is composed of 6 questions such as “how often do you go to the museum?” and “how important is art in your life?” on seven-point (Likert) scales. Finally, it was important that the participants (falsely) believed that the face research pictures we used were real artwork. Moreover, the participants in the prestige condition should believe that they belonged to the MoMA. To check this, we showed 6 pictures, 5 of which were real works of art from the MoMA that we also used as fillers and 1 of which was one of the face research stimuli. Participants had to indicate which one of these pictures they thought was not part of the MoMA collection.

Results of studies 1 and 2

In both studies, simple proportion tests revealed that participants in the MoMA condition indicated significantly less often than expected by chance that the face stimulus did not belong to the MoMA (p_{study1} = 5.3% < p_{chance} = 1/6 or 17%, $z_{study\ 1}$ = -2.55, $p < .01$ and p_{study2} 4.3% = < p_{chance} = 1/6 or 17%, $z_{study\ 2}$ = -2.78, $p < .01$), demonstrating that we successfully concealed the fact that our stimuli (face research pictures to avoid familiarity effects) did not really belong to the MoMA.

We expected that laypersons' appreciation would be positively affected by facial attractiveness, while we expected no such effect among experts. Furthermore, we expected the reverse for prestige, i.e., no effect among laypersons and a positive one among experts. Hence, we predicted an interaction between content and expertise and between prestige and expertise. However, Repeated Measures General Linear Models (RM GLM) with appreciation as a dependent variable revealed neither an interaction between expertise and prestige ($F_{study1}(1,147) = 1.51$, $p = .22$ and $F_{study2}(1,116) = 1.02$, $p = .32$) nor between expertise and content ($F_{study1}(1,147) = .24$, $p = .63$ and $F_{study2}(1,116) = .98$, $p = .33$). Furthermore, the analysis indicated a significant main effect of subjective expertise, such that appreciation increases as subjective expertise increases ($F_{study\ 1}(1,147) = 8.17$, $p < .01$ and $F_{study\ 2}(1,116) = 24.55$, $p < .01$). There was no significant main effect of prestige ($F_{study\ 1}(1,147) = .25$, $p = .62$ and $F_{study\ 2}(1,116) = .69$, $p = .41$). Interestingly, the RM GLMs did reveal a significant main effect of content in both studies ($F_{study\ 1}(1,147) = 21.18$, $p < .01$ and $F_{study\ 2}(1,116) = 19.13$, $p < .01$) such that participants appreciated the pictures more if the content (i.e., face) was attractive ($M_{study\ 1} = 3.38$, $SD_{study\ 1} = 1.14$; $M_{study\ 2} = 3.62$, $SD_{study\ 2} = 1.11$) compared to intermediate ($M_{study\ 1}$ = 2.79, $SD_{study\ 1} = 1.04$; $M_{study\ 2} = 2.83$, $SD_{study\ 2} = 1.17$).

The analysis seemed to refute our hypothesis that expertise interacts with content and with prestige. However, it appears that subjective art expertise was very low in both of these two samples, i.e., $M_{study\ 1}$ = 16.92, $SD_{study\ 1} = 7.18$ and $M_{study\ 2} = 17.70$, $SD_{study\ 2} = 6.89$, on a scale ranging from 6 to 42. Therefore, we may conclude that these two samples largely consisted of laypeople. If correct, we should still find the predicted interactions if we included subjects with more expertise, which we did in the third study.

If the majority of these participants were indeed laypeople, we would expect that the main effect of content that we found was mediated by aesthetic pleasure. Therefore, multiple regression analyses were conducted on the sample of study 2 to assess each component of the proposed mediation model (Baron & Kenny, 1986). First, we found that, consistent with the above analyses, attractive content (as opposed to intermediate content) was positively associated with art appreciation (β = .79, t (119) = 8.47, p < .01). We also found that attractive content was positively related to aesthetic pleasure (β = 1.45, t (119) = 14.58, p < .01). Lastly, the results indicated that the mediator, aesthetic pleasure, was positively associated with art appreciation (β = .63, t (119) = 18.61, p < .01). Because both the a-path and b-path were significant, mediation analyses were tested using the Sobel test (Baron & Kenny, 1986; MacKinnon, Warsi, & Dwyer, 1995; Sobel, 1982).[22] The results of the Sobel test (t = 11,48, p < .01) supported the prediction that aesthetic pleasure mediated the effect of content on art appreciation. In addition, the results indicated that the direct effect of content on art appreciation remained significant but shrank (β = .25, t (119) = 2.50, p = .01) when controlling for aesthetic pleasure, thus also supporting mediation. Figure 6 displays the results. Furthermore, to address the concern that participants did not clearly distinguish between aesthetic pleasure and appreciation, we refuted the existence of a reverse causal effect between the mediator aesthetic pleasure and the outcome variable appreciation by demonstrating that the c'-path of the reversed model differed from the original, i.e., the direct effect of content on aesthetic pleasure did not shrink when controlling for art appreciation (β = .90, t (119) = 10.68, p < .01).[23]

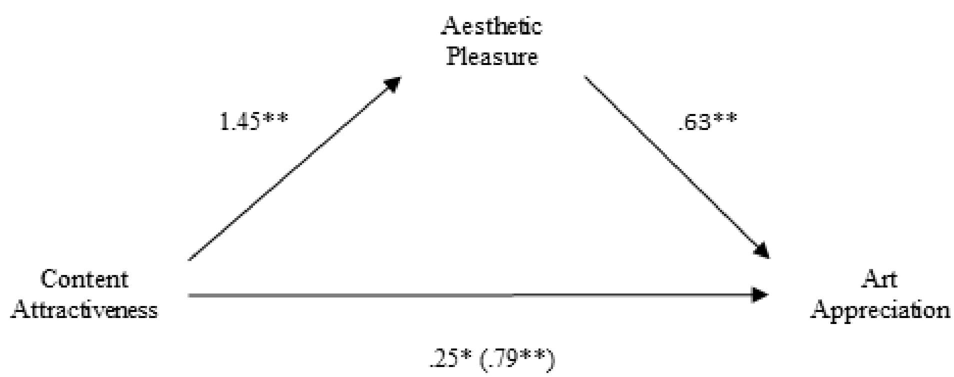

*Figure 6. Indirect effect of content attractiveness on art appreciation through aesthetic pleasure in study 2. Note: *p < .05, ** p < .01*

[22]Even though bootstrapping is becoming the most popular method to test mediation (Hayes, 2009), it is advised to use the Sobel test when testing mediation of within subjects effects, as no published bootstrapping method of such effects exists to the best of our knowledge (Andrew F. Hayes, pers. comm.; Zhao, Lynch, & Chen, 2010).

[23]In both studies, subjective expertise was higher among female ($M_{\text{study 1}}$ = 20.39, $SD_{\text{study 1}}$ = 6.42; $M_{\text{study 2}}$ = 19.87, $SD_{\text{study 2}}$ = 7.78) than male participants ($M_{\text{study 1}}$ = 14.76, $SD_{\text{study 1}}$ = 6.09; $M_{\text{study 2}}$ = 15.55, $SD_{\text{study 2}}$ = 6.48; $F_{\text{study1}}(1,150)$ = 30.56, p < .01 and $F_{\text{study2}}(1,119)$ = 10.13, p < .01)

Study 3

Methods

One hundred and six expert participants were recruited by posting the survey on the Facebook page of a Western European modern and contemporary art museum and on the Facebook page of a Western European art academy. In exchange for online participation, participants received an entrance ticket to an art exhibition. They ranged in age from 17 to 63 years (M = 36.76, SD = 12.25); 50 were male and 56 female. Eighty-seven lay participants were recruited via sports and news Facebook pages. They ranged in age from 18 to 47 years (M = 21.44, SD = 3.70); 42 were male and 45 female. In exchange for online participation, movie tickets were raffled off among them (20% chance). In this manner, we obtained two judgmental samples consisting of 193 participants in total. Participants were informed about the procedures of the study and the fact that their participation was anonymous and voluntary in the introduction screen. They agreed to participate by pressing on the 'proceed' arrow.

In this study, we repeated the methods of study 2 described above and added an objective expertise measurement in the form of a multiple choice art quiz aimed at assessing participants' knowledge about classic, modern and contemporary art (see Appendix A).

Results

We confirmed that the 2 judgmental samples differed substantially in expertise with subjective expertise, $F(1,191) = 362.04$, $p < .01$, and objective expertise, $F(1,191) = 178.32$, $p < .01$. Both measures also correlated considerably (Pearson's $r = .71$, $p < .01$), indicating that the subjective expertise measure adapted from Leder et al. (2010), which we used in the previous two studies, was valid. Consequently, after standardizing them, we combined the two variables into one expertise measure (from here on: 'expertise'), which also confirmed that the 2 samples differed in expertise, $F(1,191) = 371.65$, $p < .01$. As the distributions barely overlapped, we used sample as a grouping variable for expertise. Appendix B summarizes the results. A simple proportion test revealed that participants in the MoMA condition indicated significantly less often (p = 3.3%) than expected by chance (p = 1/6 = 17%) that the face stimulus did not belong to the MoMA (z = -3.44, p < .01), demonstrating that we were successful in concealing that our stimuli in fact did not belong to the MoMA.[24]

RM GLM with sample as a dummy variable reflecting expertise level revealed a significant interaction between expertise and content, $F(1,189) = 42.71$, $p < .01$, as predicted. Simple contrast tests showed that this effect was not only caused by the fact that laypersons appreciated artwork of attractive faces (M = 3.79, SD = 1.16) more than those of intermediate faces (M = 3.21, SD = 1.23; $F(1,189) = 38.18$, $p < .01$), which replicated the findings of studies 1 and 2, but also by the fact that experts appreciated portraits of attractive faces (M = 4.19, SD = 1.16) less than those of intermediate faces (M = 4.44, SD = 1.14; $F(1,189)$ = 8.44, $p < .01$). The analysis also revealed a marginally significant interaction between expertise and prestige, $F(1,189) = 3.24$, p =.073, as predicted. Simple contrast tests indicated that this interaction was caused by the fact that experts appreciated the pictures more when they were purportedly part of the MoMA collection (M = 4.54, SD = .91 vs. M = 4.09, SD = 1.17; $F(1,189) = 4.67$, p = .03), while laypersons' appreciation was not influenced by prestige (M = 3.44, SD = 1.26 vs. M = 3.55, SD = .98; $F(1,189)$ = .23, p = .63), both as predicted. Furthermore, the analysis indicated a main effect of sample, $F(1,189) = 27.73$, p < .01, reflecting that experts (M = 4.32, SD = 1.07) appreciated the pictures more than laypersons (M = 3.50, SD = 1.11). This result suggests again that the purported works of art were credible to experts. Of less interest, the analysis also revealed a positive main effect of content ($M_{\text{intermediate}}$ = 3.88, SD = 1.33 vs. $M_{\text{attractive}}$ = 4.01, SD = 1.18; $F(1,189) = 7.00$, $p < .01$).[25] These findings are displayed in Figure 7.[26]

---

[24] In addition, as this question was assessed of all participants, it allowed us to verify whether experts were better than laypersons at identifying that our stimuli did not belong to the MoMA. A z-test to compare two proportions revealed that experts (p = 3.8%) and laypersons (p = 8%) performed equally poor in distinguishing between real MoMA artwork used as fillers and the face research pictures used as stimuli (z = 1.3, p = .11).

[25] Adding gender to the model showed that the content effect was partially moderated by gender ($F(1,185) = 14.83$, $p < .01$) such that, as simple contrast tests indicated, men appreciated pictures of attractive faces (M = 4.16, SD = 1.15) more than those of neutral faces (M = 3.78, SD = 1.35; F = (1,185) = 22.31, p < 01) because all other contrasts were not significant. This simple effect of men is likely due to the fact that we used pictures of women's faces. Gender did not moderate the interactions of interest to our purposes, i.e., expertise and content ($F(1,185)$ = .47, p = .49) and expertise and prestige ($F(1,185)$ = .09, p = .76).

[26] RM GLM on the total sample with the continuous expertise variable yielded very similar results as with the expertise grouping variable. It revealed the predicted significant interactions between expertise and prestige $F(1,189)$ = 3.90, p = .05, and between expertise and content, $F(1,189) = 34.70$, $p < .01$. In addition, the analysis indicated a significant main effect of expertise, $F(1,189) = 18.34$, $p < .01$ and of content, $F(1,189) = 4.062$, p = .05)

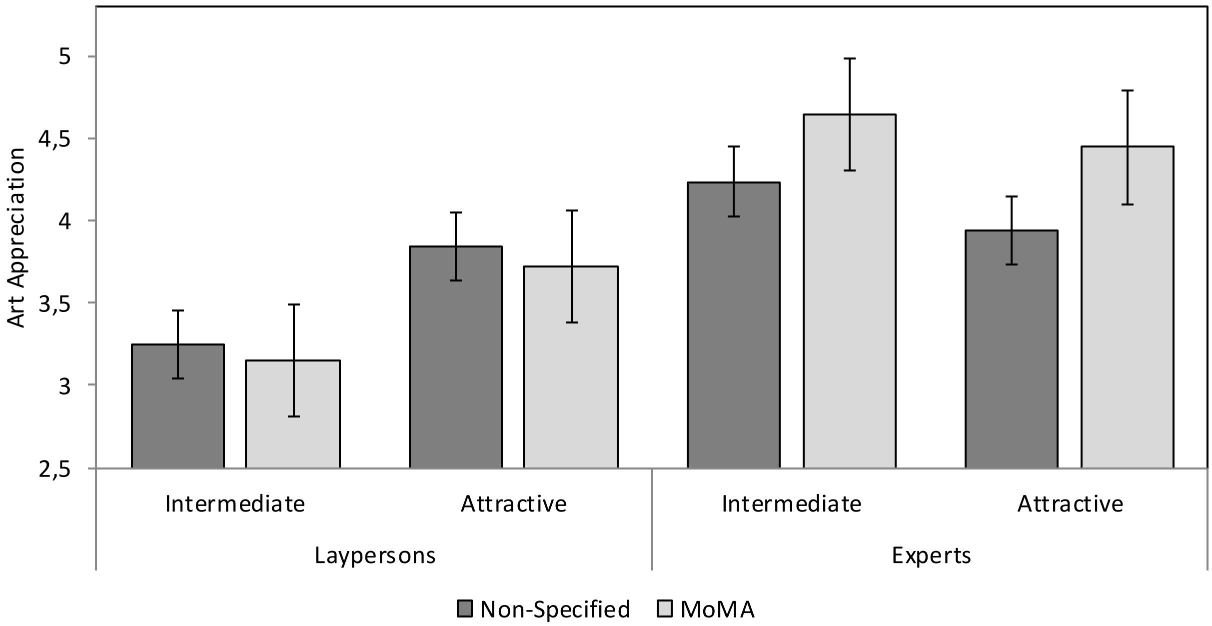

Figure 7. The effects of intermediate vs. attractive content depicted (i.e., faces) and of neutral vs. high prestige (i.e., purportedly part of the MoMA collection) on laypersons' and experts' art appreciation in study 3. Laypersons appreciated purported artwork with attractive content more, while experts appreciated them less than intermediate content. Experts were positively affected by prestige, whereas non-experts were not. The error bars show the standard error of the mean.

Subsequently, within-sample mediation analyses were conducted. To test our prediction that among laypeople, aesthetic pleasure mediated the content effect on art appreciation, multiple regression analyses were conducted on the laypeople sample to assess each component of the mediation model (Baron & Kenny, 1986). First, we found that content attractiveness was positively associated with art appreciation (β = .58, t (86) = 6.14, p < .01), consistent with the above analyses. It was also found that content attractiveness was positively related to aesthetic pleasure (β = 1.17, t (86) = 10.39, p < .01). Lastly, the results indicated that the mediator, aesthetic pleasure, was positively associated with art appreciation (β = .49, t (86) = 10.36, p < .01). Because both the a-path and b-path were significant, mediation analyses were tested using the Sobel test (Baron & Kenny, 1986; MacKinnon, Warsi, & Dwyer, 1995; Sobel, 1982). The results of the Sobel test (t = 7.34, p < .01) support the prediction that aesthetic pleasure mediates the effect of content on art appreciation among laypeople. In addition, the results indicated that the direct effect of content on art appreciation shrank and virtually became zero and non-significant (β = .02, t (86) = 0.16, p = .88) when controlling for aesthetic pleasure, thus also suggesting mediation. Figure 8 (Panel A) displays the results. Furthermore, we refuted the existence of a reverse causal effect between the mediator aesthetic pleasure and the outcome variable appreciation by demonstrating that the b-path of the reversed model differed from the original, i.e., the direct effect of content on aesthetic pleasure did not shrink and remained significant when controlling for art appreciation (β = .84, t (86) = 7.51, p < .01).

To test our prediction that among experts, the prestige effect on art appreciation is mediated by admiration for the artist, multiple regression analyses were conducted on the expert sample to assess each component of the mediation model (Baron & Kenny, 1986). First, it was found that prestige (as opposed to neutral) was positively associated with art appreciation (β = .45, t (104) = 2.21, p < .01), consistent with the above analyses. It was also found that prestige was positively related to admiration for the artist (β = .60, t (104) = 3.17, p < .01). Lastly, the results indicated that the mediator, admiration for the artist, was positively associated with art appreciation (β = .88, t (105) = 21.97, p < .01). Because both the a-path and b-path were significant, mediation analyses were tested using the Sobel test (Baron & Kenny, 1986; MacKinnon, Warsi, & Dwyer, 1995; Sobel, 1982). The results of the Sobel test (t = 3.14, p < .01) supported the prediction that admiration for the artist mediated the effect of prestige on art appreciation among experts. In addition, the results indicated that the direct effect of prestige on art appreciation shrank and became close to zero and non-significant (β = -.09, t (104) = -0.93, p = .35) when controlling for admiration for the artist, thus also suggesting mediation. Figure 8 (Panel B) displays the results. Furthermore, we refuted the possibility that the mediator admiration for the artist may be caused by the outcome variable appreciation (i.e., feedback model or reverse causal effect) by showing that the c'-path of the reversed model differed from the original, i.e., the direct effect of prestige on admiration did not shrink and remained significant when controlling for art appreciation (β = .26, t (104) = 2.85, p < .01).

As a final check, we verified whether aesthetic pleasure mediated a content effect among experts and whether admiration mediated a prestige effect among laypeople. To comply with our predictions, both should not be the case. With respect to the former, although a significant negative association between content and appreciation was found (β = -.25, t (105) = 2.97, p < .01), consistent with the above analyses, content did not relate to aesthetic pleasure among experts, as its coefficient was near zero and not significant (β = 0.12, t (105) = 1.11, p = 0.27), thus excluding mediation. With respect to the latter, as there was not even a total effect of prestige on appreciation among laypeople (β = -.11, t (85) = -.48, p = 0.63), mediation was also excluded.

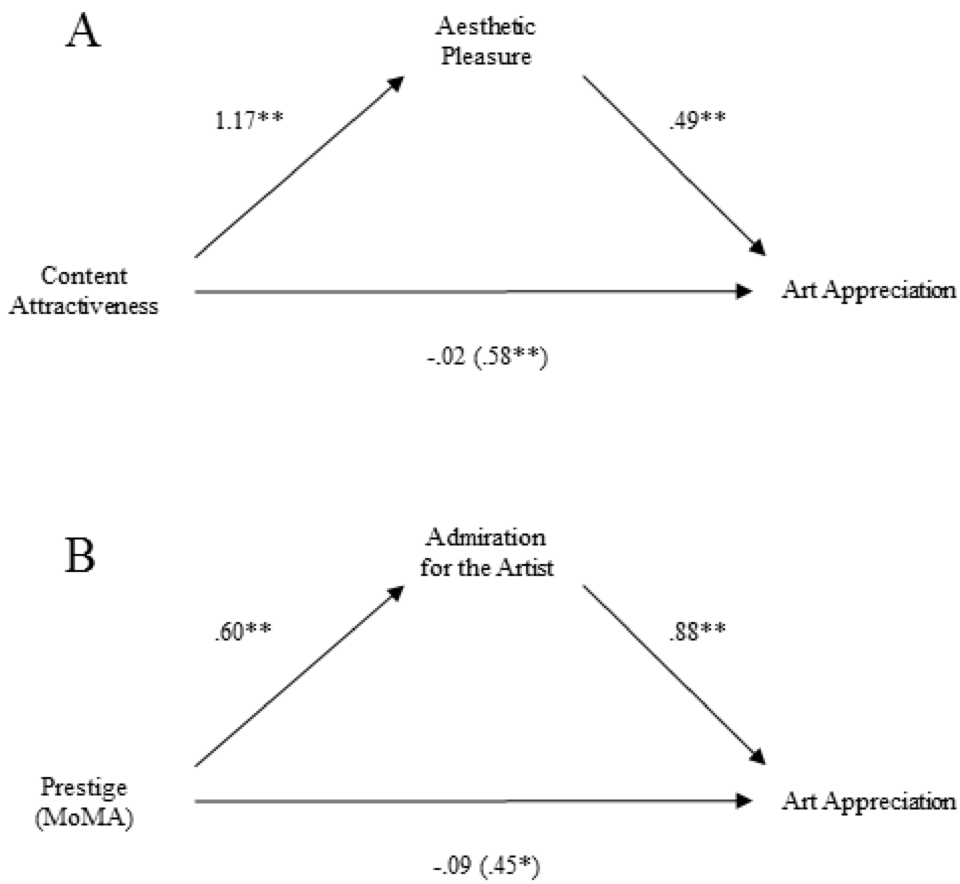

*Figure 8. Study 3: A. Indirect effect of content on art appreciation among laypeople through aesthetic pleasure; B. Indirect effect of prestige on art appreciation among experts through admiration for the artist. Note: *p < .05, ** p < .01*

Discussion

It has been suggested that art is a type of pleasure technology that succeeds by exploiting individual's evolved aesthetic preferences (Pinker, 1997, 2007). As such, spectators may trade off rewards from indulging in art and biological activities, resulting in less effort being allocated to reproduction (Enquist et al., 2002). Here, we investigated whether, as a consequence, art experts (i.e., artists, art critics, museum directors, etc.), typically exposed to high doses of art, would have socially learned to resist exploitation. As prestige bias may trump content biases (Henrich & Boyd, 2002), we postulated that experts would achieve this by selectively preferring art from prestigious artists (Henrich & Gil-White, 2001). Studies 1 and 2 showed in the controlled setting of the laboratory that laypersons (the general audience) appreciate artwork depicting attractive faces more than intermediate faces. Study 3 replicated this in an online setting in a sample with a low level of art expertise. Study 2, also conducted in the laboratory, showed that, in addition, this was on account of the fact that laypersons find attractive faces to be more aesthetically pleasing. Prestige did not affect laypersons' appreciation. Because perceiving facial attractiveness probably evolved to be rewarding to optimize social partner and mate choice (Little, Jones, & DeBruine, 2011), these findings support the hypothesis that art exploits pre-existing evolved aesthetic preferences of the general audience (Pinker, 1997, 2007). In study 3, real art experts participated in addition to laypersons. The results of study 3 replicated the findings of studies 1 and 2 regarding laypersons and indicated that by contrast and as predicted, expert appreciation was positively affected by prestige (i.e., when the artwork purportedly belonged to the permanent collection of the MoMA). This prestige effect was mediated by admiration for the artist, rather than aesthetic pleasure (Henrich & Gil-White, 2001).

Study 3 showed that experts confer lower appreciation to portraits of attractive faces than to portraits of moderately attractive faces, which further corroborates our contention that expertise and the use of prestige is associated with resistance against beautiful content that exploits evolved preferences. Similarly, recent research showed that compared to laypersons, experts exhibit attenuated emotional responses to content features of artwork and they like negative content more (Leder et al., 2013). However, caution is warranted. Other possible explanations of the negative content effect among experts cannot be ruled out by the present data. We distinguish a number of additional, non-mutually exclusive explanations. First, the negative content effect may be caused by a preference for neutrally attractive content rather than avoidance of beauty. Neutrally attractive content, being less immediately rewarding, may be more thought-provoking, eliciting questions regarding the artist's intentions (Bullot & Reber, 2013; Davies 2013; De Smedt & De Cruz, 2013). The cognitively oriented learning attitude of experts may drive them to thought-provoking stimuli in the art domain (Leder et al., 2012; Silvia, 2009). Second, experts may want to secure distinctiveness, employing their art appreciation as a badge of group membership and expertise that distinguishes them from laypersons (Bourdieu 1979; cf. Boyd & Richerson, 1987; Pinker 1997). Being an expert may not make much sense if expert appreciation does not differ from that of laypersons. Third, the negative content effect may be the result of the prestige bias process without the purpose of resistance against exploitation; if neutral content is associated with success and prestige in the art domain for some other reason, experts may also have learned to prefer neutral content on account of its association with prestige. Further research is required to disentangle the respective influences of these processes on experts' art appreciation.

At first glance, our finding that laypersons (i.e., outsiders of the art domain, a group that turned out to be quite large compared to experts) do not employ prestige bias seems to go against the logic of the mechanism. After all, especially naïve individuals should benefit from employing it, as it is assumed to be an effective strategy to efficiently acquire "better-than-average" information from successful experts in a domain (Henrich & Gil-White, 2001). For example, field research showed that individuals from a small-scale society were biased to learn from others perceived as more prestigious, both within and across three cultural domains (i.e., fishing, growing yams, and using medicinal plants) (Henrich & Broesch, 2011). However, it has been suggested that content bias may suppress prestige bias (Claidière & Sperber, 2007). Specifically, laypersons, who are both less exposed (and therefore less prone to its negative fitness effects) and more vulnerable to exploitation due to lower expertise, may not resist the immediate rewards of beautiful content, even though they would ultimately benefit from employing prestige bias instead. Moreover, findings suggest that individuals from large-scale societies choose not to employ prestige bias if they think it will not pay off (Martens & Tracy, 2013). The contention that employing prestige bias often does not pay off for naïve individuals of large-scale societies seems to make sense as the number of specialized cultural domains is exceedingly larger at large scales compared to small-scale societies, while the individual cognitive capacity to acquire domain specific expertise should be about the same. Therefore, it might be that individuals in small-scale societies, who are exposed to only a few domains of specialization may on average employ prestige bias much more often for any given domain than individuals in large-scale societies. The pattern our study reveals (i.e., prestige bias trumps content bias as expertise increases) raises the question of whether it is specific to the domain of visual art or whether it applies more generally. For example, research has suggested that music, language, and writing have also evolved by exploiting pre-existing preferences of human evolved psychology (Changizi, Zhang, & Shimojo, 2006; Changizi, 2011). Perhaps in these cultural innovations, signs of resistance against exploitation associated with expertise and prestige bias can be found as well. Following the above, we expect resistance associated with prestige bias to be more likely (1) the smaller the number of cultural domains the individual is exposed to (i.e., small-scale as opposed to large-scale society) and (2) the higher the costs associated with exploitation. Further research may reveal whether this is the case for these and other domains of human culture. If generalizable, the present research may provide a different angle to the ongoing debate about whether content (a.k.a. cultural attractors) or context biases (such as prestige) are the main drivers of cultural evolution (Claidière & Sperber, 2007; Henrich & Boyd, 2002; Henrich & McElreath, 2003), by suggesting that expertise, as a moderator, affects their relative importance.

Incidentally, our results indicated that experts are as poor as laypersons at distinguishing between MoMA artwork and face research pictures. This may come as a surprise as one would expect experts to know better than laypersons how to tell real art from fake art, certainly if the art belongs to one of the most influential museums in the world, the MoMA. As mentioned, our results also indicated that experts (but not laypersons) appreciate exactly the same (purported) works of art more if they are (purportedly) part of the prestigious MoMA collection than if no such information is given (note that we concealed its assessment as prestige was manipulated between subjects). At first sight, these findings do not paint a very flattering image of art expertise. However, they make sense from a social learning perspective. First, an important assumption of prestige bias is that it enables acquisition of expertise in a domain that is difficult to obtain on one's own. Therefore, individuals should trustingly copy the cultural repertoire of prestigious individuals, as prestige is expected to generally reliably correlate with expertise, even though this may not always be the case (Boyd & Richerson, 1985; Boyd & Richerson, 2007; Henrich and Gil-White, 2001). This thus explains the finding that experts credulously confer higher appreciation to artwork from prestigious artists as indicated by their presence in the MoMA collection. Second, as the amount of aesthetic pleasure is no longer the criterion upon which expert appreciation is based, anything can be art, as long as it belongs to a recognized art context (Danto, 2003). This may explain why experts do not distinguish between face research pictures and art from the MoMA. On the one hand, any artifact could be a work of art from the MoMA. On the other hand, face portraits, albeit research pictures, when placed in an art context, will spontaneously be considered genuine art by experts (Dickie, 1974).

Our study provides a previously unconsidered explanation for the fact that, while the general audience went on to prefer aesthetically pleasing (popular) art, aesthetic appeal began to lose its central position in contemporary Western (high) art since the beginning of the 20^{th} century (Danto, 2003). In so doing, this research may also contribute to bridging the infamous gap between the sciences and humanities (Snow, 1959; Wilson, 1999). Specifically, several prominent adherents of an evolutionary approach to the arts have dismissed modern Western art as unnatural or problematic and claimed that this warrants evolutionists to ignore it (Dutton, 2006; Miller, 2000; Pinker, 1997). Conversely, many scholars from the humanities have not taken evolutionary approaches seriously because what evolutionists called problematic were to them the hallmarks of art history, such as Duchamp's Fountain. However, employing cultural evolution theory, this research demonstrates that evolution can take into account recent developments in art appreciation and production (cf. Morin, 2013). This research thus illustrates that cultural evolution theory may shed light on evolutionary processes as well as historical time scales (Boyd & Richerson, 1992).

Acknowledgments

Many thanks to the members of the Research Centre for Marketing and Consumer Science at the University of Leuven for commenting on these studies on various occasions. A special thanks to Anouk Festjens for help in the laboratory and with analyses. Thanks as well to the members of the Ethology group at the University of Antwerp for their comments. Special thanks to Morgan David and Yannick Joye for commenting on a draft of the paper and to Els Van Peborgh, Sam Franssens and Andreas De Block for discussion. This paper was supported by the Research Foundation Flanders (FWO; Grant no. G085012N).

References

Baron, R. M., & Kenny, D. A. (1986). The moderator-mediator variable distinction in social psychological research: Conceptual, strategic, and statistical considerations. *Journal of Personality and Social Psychology*, 51, 1173-1182.

Barrett, H.C. (2005). Adaptations to predators and prey. In D. M. Buss (Ed.), *The Handbook of Evolutionary Psychology* (pp. 200–223). New York: Wiley.

Bourdieu, P. (1979). *Le Sens Commun: La Distinction Critique Sociale Du Jugement.* Paris: Les Editions de Minuit.

Boyd, R., & Richerson, P. (1985). *Culture and the evolutionary process*. Chicago: The University of Chicago Press.

Boyd, R., & Richerson, P. (1987). The Evolution of Ethnic Markers. *Cultural Anthropology*, 2, 65–79.

Boyd, R., and Richerson, P.J. (1992). How microevolutionary processes give rise to history. In M. Niteki & D. Niteki (Eds.), *History and Evolution* (pp. 149–178), Albany: State University of New York Press.

Boyd , R., & Richerson , P. (2007). Culture, adaptation, and innateness. In P. Carruthers, S. Stich & S. Laurence, *The Innate Mind: Culture and Cognition*, Oxford : Oxford University Press.

Bullot, N. J., & Reber, R. (2013). The artful mind meets art history: Toward a psycho-historical framework for the science of art appreciation. *Behavioral and Brain Sciences*, 36(02), 123-137. doi:10.1017/S0140525X12000489

Changizi, M. A., Zhang, Q., Ye, H., & Shimojo, S. (2006). The structures of letters and symbols throughout human history are selected to match those found in objects in natural scenes. *The American Naturalist*, 167(5), 117–139.

Changizi, M. (2011). *Harnessed: How language and music mimicked nature and transformed ape to man*. Dallas, TX: Benbella Books.

Claidière, N., & Sperber, D (2007). The role of attraction in cultural evolution. *Journal of Cognition and Culture*, 7, 89-111.

Danto, A. (2003). *The abuse of beauty: aesthetics and the concept of art*. Chicago: Open Court.

Davies, S. (2013). Artists' intentions and artwork meanings: Some complications. *Behavioral and Brain Sciences*, 36, 138-139. doi:10.1017/S0140525X12001598.

de Nooy, W. (2002). The dynamics of artistic prestige. *Poetics*, 30, 147-167.

De Smedt, J., & De Cruz, H. (2012). Human artistic behavior: adaptation, byproduct, or cultural group selection? In K. Plaisance & T. Reydon (Eds.), *Philosophy of Behavioral Biology* (pp. 167-187). Boston Studies in the Philosophy of Science, 282 (4).

De Smedt J., De Cruz H. (2013). The artistic design stance and the interpretation of Paleolithic art. *Behavorial and Brain Sciences*, 36, 139-140. 10.1017/S0140525X12001847

Dickie, G. (1974). *Art and the aesthetic: an institutional analysis*. New York: Cornell University Press.

Dutton, D. (2006). A naturalist definition of art. *Journal of Aesthetics and Art Criticism*, 64, 367-377.

Dutton, D. (2009). *The art instinct: Beauty, pleasure and human evolution*. Oxford: Oxford University Press.

Enquist, M., Arak, A., Ghirlanda, S., & Wachtmeister, C. A. (2002). Spectacular phenomena and limits to rationality in genetic and cultural evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 357, 1585-1594.

Falk, J.H., & Balling, J.D. (2010). Evolutionary influence on human landscape preference. *Environment and Behavior*, 42, 479-493.

Hayes, A. F. (2009). Beyond Baron and Kenny: Statistical mediation analysis in the new millennium. *Communication Monographs*, 76, 408-420.

Henrich, J., & Boyd, R. (2002). On modeling cognition and culture. *Journal of Cognition and Culture*, 2, 87-112.

Henrich, J., & Gil-White, F.J. (2001). The evolution of prestige: freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior*, 22, 165–196.

Henrich, J., & Broesch, J. (2011). On the nature of cultural transmission networks: evidence from Fijian villages for adaptive learning biases. *Philosophical Transactions Of The Royal Society B: Biological Sciences*, 366(1567), 1139-1148. doi:10.1098/rstb.2010.0323

Henrich, J., & McElreath, R. (2003). The evolution of cultural evolution. *Evolutionary Anthropology*, Evolutionary Anthropology, 12, 123-135. DOI 10.1002/evan.10110

Johnstone, R. (2002). Signalling Theory: Signal Design and Selection for Efficient Displays, Coevolution Between Signaller and Receiver. In M. Pagel (Ed.), *Encyclopedia of Evolution*, Oxford University Press.

Leder, H., Gerger, G., Brieber, D., & Schwarz, N. (2013). What makes an art expert? Emotion and evaluation in art appreciation. *Cognition & Emotion*, 1-11. doi:10.1080/02699931.2013.870132

Leder, H., Gerger, G., Dressler, S., & Schabmann, A. (2012). How art is appreciated. *Psychology of Aesthetics, Creativity, and the Arts*, 6, 2-10.

Little, A., Jones, B., & DeBruine, L. (2011). Facial attractiveness: evolutionary based research. *Philosophical Transactions Of The Royal Society B*, 366(1571), 1638-1659.

MacKinnon, D. P., Warsi, G., & Dwyer, J. H. (1995). A simulation study of mediated effect measures. *Multivariate Behavioral Research*, *30*, 41-62.

Martens, J. P., & Tracy, J. L. (2013). The Emotional Origins of a Social Learning Bias: Does the Pride Expression Cue Copying? *Social Psychological And Personality Science*, 4(4), 492-499. doi:10.1177/1948550612457958

Miller, G. (2000). *The mating mind*. London: Heinemann.

Miller, G. (2006). Runaway consumerism explains the Fermi Paradox. The Edge Foundation. Retrieved December, 2014, from https://edge.org/response-detail/11475

Morin, O. (2013). How portraits turned their eyes upon us: Visual preferences and demographic change in cultural evolution. *Evolution And Human Behavior*, 34(3), 222-229. doi:10.1016/j.evolhumbehav.2013.01.004

Nakamura, K., Kawashima, R., Nagumo, S., Ito, K., Sugiura, M., Kato, T., et al. (1998). Neuroanatomical correlates of the assessment of facial attractiveness. *NeuroReport*, 9, 753-757.

New, J., Cosmides, L., & Tooby, J. (2007). Category-specific attention for animals reflects ancestral priorities, not expertise. *Proceedings of the National Academy of Sciences, 104*, 16598-16603.

Orians, G.H., & Heerwagen, J.H. (1992). Evolved responses to landscapes. In J.H. Barkow, L. Cosmides & J. Tooby (Eds.), *The adapted mind. Evolutionary psychology and the generation of culture* (pp.555–579). New York: Oxford University Press.

Pinker, S. (1997). *How the Mind Works.* New York: W. W. Norton.

Pinker, S. (2007). Toward a consilient study of literature. *Philosophy and Literature*, 31, 162-178.

Schacht, A., Werheid, K., & Sommer, W. (2008). The appraisal of facial beauty is rapid but not mandatory. *Cognitive, Affective, & Behavioral Neuroscience*, 8 (2), 132-142.

Silvia, P.J. (2009). Looking past pleasure: Anger, confusion, disgust, pride, surprise, and other unusual aesthetic emotions. *Psychology Of Aesthetics, Creativity, And The Arts*, 3(1), 48-51.

Snow, C. P. (2001) [1959]. *The Two Cultures*. London: Cambridge University Press.

Sobel, M. E. (1982). Asymptotic intervals for indirect effects in structural equations models. In S. Leinhart (Ed.), *Sociological methodology* (pp.290-312). San Francisco: Jossey-Bass.

Thornhill, R. (2003) Darwinian aesthetics informs traditional aesthetics. In K. Grammer & E. Voland (Eds), *Evolutionary Aesthetics* (pp. 9-38). Berlin: Springer-Verlag.

Wilson, E. O. (1999). *Consilience*. New York: Vintage Books

Windhager, S., Atzwanger, K., Bookstein, F.L., & Schaefer, K. (2011). Fish in a mall aquarium—An ethological investigation of biophilia. *Landscape and Urban Planning, 99*, 23-30.

Winston, J. S., O'Doherty, J., Kilner, J. M., Perrett, D. I., & Dolan, R. J. (2007). Brain systems for assessing facial attractiveness. *Neuropsychologia*, 45, 195-206.

Wong, B. B. M., Salzmann, C., & Schiestl, F. P (2004). Pollinator attractiveness increases with distance from flowering orchids. *Proceedings Of The Royal Society B: Biological Sciences*, 271(Suppl_4), S212-S214. doi:10.1098/rsbl.2003.0149

Wong, B. B.M. & Schiestl, F. P. (2002). How an orchid harms its pollinator. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 269, 1529–1532.

Yang, J., Wang, A., Yan, M., Zhu, Z., Chen, C., & Wang, Y. (2012). Distinct Processing for Pictures of Animals and Objects: Evidence From Eye Movements. *Emotion*. Advance online publication. doi: 10.1037/a0026848

Zhao, X., Lynch, J., Jr., & Chen, Q. (2010). Reconsidering Baron and Kenny: Myths and Truths about Mediation Analysis. *Journal Of Consumer Research*, 37(2), 197-206. doi:10.1086/651257

Appendices

Appendix A

The multiple choice art quiz consisted of ten questions. One question was the above described check of whether the fact that the face stimuli did not belong to the MoMA was successfully concealed; this question did not count for the expertise score. In seven of the remaining nine questions, we asked who created the visual artwork that was displayed, ranging from Renaissance art (Bruegel's The Tower of Babel) up to contemporary art (e.g., Damien Hirst's The Physical Impossibility of Death in the Mind of Someone Living) and variably being a painting, an installation, or a performance. One question was who painted the Mona Lisa and another involved putting art genres in chronological order. With the exception of the latter, all questions were multiple choice, offering 4 or 5 options, including an "I don't know" option.

Appendix B

Table 1. Summary of the results of study 3.

		Sample		
		Laypersons	Experts	Total[a]
Appreciation[b]	Mean (SD)	3.50 (1.20)	4.32 (1.15)	3.91 (1.18)
	Range	1 – 6.5	1 – 7	
Aesthetic pleasure[b]	Mean (SD)	3.43 (1.22)	4.28 (1.12)	3.86 (1.16)
	Range	1 – 6	1 – 7	
Admiration[b]	Mean (SD)	3.40 (1.16)	4.11 (1.10)	3.76 (1.13)
	Range	1 – 7	1 – 6.5	
Appreciation = Aesthetic pleasure	β	.49 [e]	0.85 [e]	
Appreciation = Admiration	β	.73 [e]	.82 [e]	
Subjective Expertise[c]	Mean (SD)	17.25 (7.06)	33.96 (5.12)	25.61 (6.10)
	Range	6 – 32	22 – 42	
Objective Expertise[d]	Mean (SD)	3.66 (1.52)	6.92 (1.81)	5.29 (1.67)
	Range	0 – 7	1 – 9	
Correlation Objective & Subjective Expertise	Pearson's r			.71 [e]

[a] corrected for unequal size of expert and layperson samples

[b] scale range: 1 – 7

[c] scale range: 6 – 42

[d] scale range: 0 – 9

[e] significant at $p < .01$

General Discussion

Summary

In eight chapters, I aimed to contribute to shedding light on the arts and their appreciation from an evolutionary perspective. In the first two chapters I critically evaluated the evidentiary criteria from standard evolutionary psychology some existing accounts employ to demonstrate that art qualifies as a human biological adaptation. I argued that these criteria do not suffice to make that claim. Furthermore, I made the case for a *cultural* evolutionary approach to the arts. One commonly used evidentiary criterion for art as adaptation is the "tight fit" between art and human cognition, which is interpreted as suggesting that cognition has undergone selection to produce and appreciate art. However, disentangling cultural and genetic evolution allows formulating the alternative hypothesis that art has evolved culturally to match human cognition. In chapter three, Derek Hodgson and I observed that in ancient and modern hunter gatherer societies, artistic activities are virtually always associated with ritual. We discussed what this implies for the adaptive significance of art. Specifically, if the arts have culturally evolved in function of ritualistic purposes, their adaptive value has depended on the adaptiveness of ritual (and whether ritualistic activities are adaptive, is still debated).

In the second part of this dissertation (chapters 4 – 6), Yannick Joye and I turned to architecture, which is one of the arts that has hardly been investigated from a biological and evolutionary perspective. In chapter four, employing the cross-species comparative approach, we investigated two main purposes human architecture has in common with nonhuman animal construction: protection and signaling. Based on the phylogenetic approach we established that protection may have been the primary function of building aptitudes in human evolution, and that building was later co-opted for signaling purposes. Subsequently, we comparatively evaluated the role of signaling models (arbitrary coevolution, sensory exploitation and costly signaling) in the cultural evolution of architectural aesthetics. In chapter five, we combined insights from environmental psychology, niche construction and cultural evolution theory to develop the hypothesis that a function of religious monumental architecture may have been to support – or even to galvanize – social learning. In chapter six, we connected the account developed in chapter five to the cognitive science of religion. We complemented the frequently held view that religious monumental architecture is a costly signal with the mechanism of sensory exploitation. We attempted to demonstrate that by exploiting the emotional response of awe in religious followers, religious monumental architecture promotes and regulates prosocial behavior and creates in them an openness to adopt supernatural beliefs.

In the final part of this dissertation, we dealt with the evolution of visual art, paying again special attention to cultural evolution and the explanatory value of sensory exploitation. In chapter seven, Mark Nelissen and I asserted that the relatively late appearance of figurative art (around 45 thousand years ago) in the course of human evolution may be attributed to an increase in the number of social learning opportunities within and between human populations at that time. We supported this assertion with archaeological data that indicate overall population growth and increased population densities at that time. These demographic changes, we argued, have allowed the retention and accumulation of innovations required for figurative art making (e.g., learned aspects of figurative drawing and pigment processing). Contrary to previous accounts, we furthermore aimed to show that this process does not require figurative art to have served adaptive purposes. Employing sensory exploitation, we established that figurative art could have evolved by exploiting pre-existing biases of evolved psychology. The dominant themes of upper Paleolithic and late stone age figurative art, animals (predators and preys) and humans (e.g., "Venus" figurines), seem to support this contention. In the final and eighth chapter Siegfried Dewitte and I present a number of experimental studies we conducted to verify whether contemporary art experts would have socially learned to resist exploitation of evolved psychology. One aspect of art's exploitative power may be that it elicits aesthetic pleasure by pushing "pleasure buttons" that evolved for other purposes. Consequently, spectators may trade-off rewards from indulging in art and biological activities, resulting in less effort being allocated to reproduction. We contend that, while the general audience (i.e., laypersons) may indeed be exploited, experts (i.e., artists, art critics, etc.), who are typically being exposed to high doses of art, may have socially learned to resist exploitation by selectively preferring art from prestigious art contexts (i.e., prestige bias). The latter would be in line with the claim that prestige bias may trump (aesthetic) content biases of evolved psychology. The results of three experimental studies support our contention. We found that laypeople's art appreciation is positively affected by a content bias for attractive faces, mediated by aesthetic pleasure, whereas experts' appreciation is positively affected by prestige and mediated by admiration for the artist. Moreover, experts confer lower appreciation to attractive compared to moderately attractive content, which is consistent with our contention that expertise and the use of prestige are associated with resistance against beautiful content that exploits evolved preferences. This research thus suggests that expertise moderates content and context (prestige) biases, which may be of relevance to an ongoing debate about their relative importance as drivers of cultural evolution. In addition, this study provides a tentative but novel explanation for the fact, famously established by philosopher Arthur Danto (2003), that beauty lost its central position in Western art during the 20th century. However our findings cannot exclude alternative explanations for the fact that art expert appreciation deviates from evolved aesthetic preferences. Further research may experimentally assess the role of prestige bias and resistance as drivers of this deviation versus other, previously suggested, potential processes. For example, preferences of experts may deviate on account of the fact that art serves as a badge of elite group membership and thus expert art appreciation as a means to distinguish oneself from the masses. Alternatively, art experts may seek intellectual challenges instead of pushing pleasure buttons. In the following section I will discuss how these different hypotheses could be experimentally verified. In addition, I will discuss how insights from sexual selection research may help elucidating the different processes at play in cultural evolution and particularly in the cultural evolution of art appreciation.

Future Directions

The chapters in this dissertation attest to the cultural nature of our species. Our behavior does not only depend on "what is in our genes," or what we learn by trial-and-error. We rely heavily on information we acquire by learning from others. But people do not just believe anything or anyone. Even though we are often eager to learn from others, we generally do not just blindly copy anyone's behavior. Thus, one of the central questions cultural evolution theory has to answer is how we decide when, who and what to copy. The answer to this question relates to the two major categories of biases or rules cultural evolution theory asserts that learners use to acquire cultural information: content and context biases. Content biases arise from the interaction of human evolved psychology and the characteristics associated with the information being transmitted (i.e., what to copy). Standard evolutionary psychology and cognitive anthropology regard this bias the main cause of cultural change and stability. For example, such content biases seem to account for at least some universals in art appreciations. By contrast, cultural evolution researchers contend that context biases explain most of the (artistic and other) variation that cultural evolution theory should track. Context biases arise from cognitive mechanisms that influence the salience and likelihood of transmission of a cultural variant based on either characteristics of the person modeling the behavior (e.g., success and prestige biases) or the distribution of traits in the population (frequency-dependent biases) (i.e., who and when to copy). In Chapters 7 and 8 and Appendix 2 of this dissertation, I have tried to spell out how the two types of biases are relevant for evolutionary aesthetics and for the biology, psychology and philosophy of art appreciation. This conclusion is meant to sketch how one can develop a couple of interesting lines of research that follow quasi-organically from the findings presented in these chapters. Hereby, I will focus primarily on how content- and context-biases interact in cultural evolution in general and in the evolution of art in particular. A few notable exceptions notwithstanding, little theoretical and empirical attention has been paid to elucidating how content and context biases relate to each other. Yet, their relations (e.g., whether they are opposing or complementing influences) affect the course of cultural evolution. For example, certain content biases (e.g., sweet tooth) may become culturally exploited, and socially learned resistance against it may be in part driven by prestige bias (e.g., influential individuals eating low-carb diets). To shed a preliminary light on this pivotal issue, I will use, on the one hand, sexual selection theory as a source of empirical and theoretical insights relevant to the issue. On the other hand, I will also point at the relevance of this relation for a deep understanding of the evolution of art.

Direct and indirect sexual and cultural selection.

As I have explained elsewhere (Appendix 2; Chapter 7), sexual selection theory constitutes a valuable source of information when it comes to the issue of how content and context bias relate to each other. This is so because it has been dealing with a strikingly similar issue, and, compared to cultural evolution theory, there has been put considerable more effort into solving it. A central concept within sexual selection theory is mate choice. Mate choice causes selection on the opposite sex. Extravagant male display traits, such as the peacock's tail, are the most apparent example that result from this process. Mate choice thus drives intersexual selection just as social learning drives cultural evolution. Importantly, mate choice has in common with social learning that sexual choosers also need to decide when, who and based on which characteristics to mate. As a result, the same two major categories of biases that feature in cultural evolution theory, i.e., content and context bias, are central to sexual selection theory as well. The mate choice equivalent of context bias is indirect benefit. The indirect benefit model asserts that mates are chosen on the basis of sexual traits that reliably indicate fitness (e.g., peacock's tail), much as cultural models from whom to learn are chosen on the basis of traits that reliably indicate better-than-average cultural information (e.g., prestige). This equivalence is uncontroversial, because formal models of indirect benefit mate choice were initially borrowed by cultural evolution pioneers to model context bias. By contrast, the concept of content bias has been developed independently from sexual selection theory. Content bias seems to correspond to sensory exploitation (a.k.a. sensory drive/trap, and receiver psychology). Sensory exploitation is a well-established and intensively researched phenomenon in behavioral ecology. As I have explained in detail in Chapter 7 and Appendix 2, the sensory exploitation model principally predicts that mate preferences result from selection on the perceptual and cognitive system of the chooser for functions in other contexts, such as finding food or avoiding becoming it and that males have evolved to exploit these preferences. In that sense, it predicts that preferences of choosers evolve because of their direct effects on fitness. This contrasts with indirect benefit, where choosers' preferences are indirectly selected on account of their correspondence to the senders' fitness. This commonality between content bias and sensory exploitation can probably boost our understanding of content bias. Signaling theory and signal detection theory seek to uncover general principles of receiver's responses and may therefore be equally applicable to mate choice and social learning. I give just two example that clarifies how this cross-fertilization may proceed. First, in recent years, several empirical and theoretical advancements have been made towards understanding how sensory exploitation relates to indirect benefit. Indirect benefit consists in fact of two major processes that also can be modeled separately, i.e., Fisher's process (a.k.a. sexy son) and good genes (a.k.a. Zahavi's handicap prin ciple). The Fisher's process predicts that mate choice is indirectly selected on account of its correlation with attractiveness of the opposite sex's same-sex offspring (i.e., "sexy sons"). By contrast, good genes predicts that mate choice is (additionally) indirectly selected on account of its correlation with the opposite sex's offspring viability (i.e., sons and daughters). The initial account of prestige bias borrowed both the formal models of good genes and Fisher's process, however in later literature the latter became neglected. Meanwhile, research has shown that, for example, it can be predicted whether sensory exploitation and good genes will be opposing or complementing (in the latter case it may be sensory drive). This suggests that the same applies to content bias and context bias, and is therefore very informative for cultural evolution theory. To the best of my knowledge, such predictions have not been considered yet. Secondly, one could explore and scrutinize the relation between content and context biases through with the help of a model that integrates direct and indirect selection. Figure 9 provides a first tentative sketch of such an integrated model for (A) sexual selection and (B) cultural evolution.

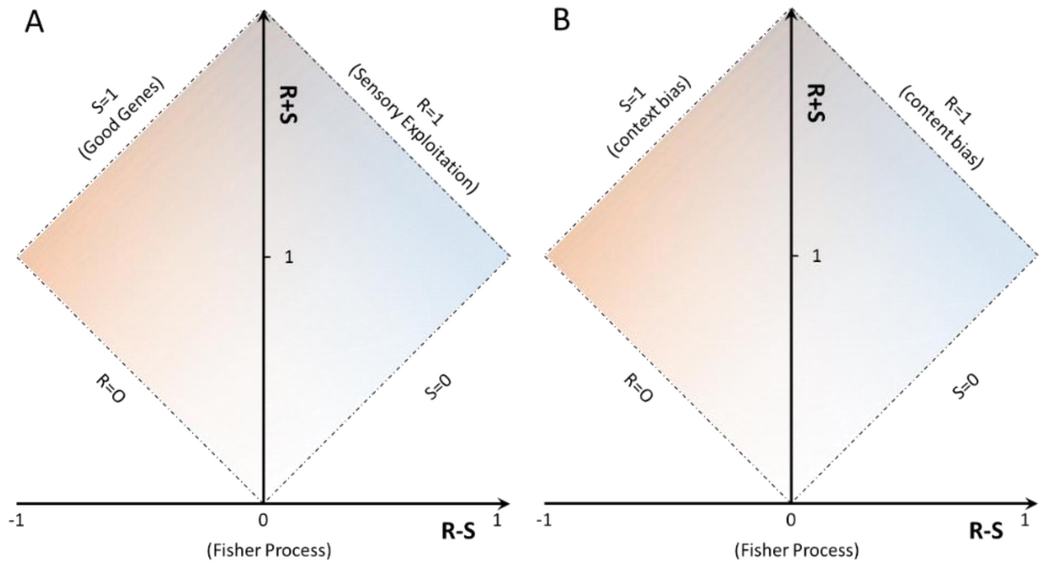

Figure 9. Integrated model for (A) sexual selection and (B) cultural evolution. S = Correlation coefficient of receiver's preference with sender viability; R = Correlation coefficient of receiver's preference with viability in all but the domain at hand. (Note that only positive correlations are included. However, an extension of the model with negative correlation coefficients is possible.)

The graph is intended to conveniently represent how direct and indirect selection interact. It maps all (theoretical) possible relations of the three existing models (Fisherian/cultural runaway, sensory exploitation/content bias, and good genes/context bias) as a function of the correlations of the receiver's response with viability of the sender and with its own viability in all but the domain at hand. In its current form, it illustrates that the receiver's preference depends on the strength of the respective correlations and the directions of the selection pressures they represent, which is an empirical issue. At first glance, it already seems to allow to make or support some predictions. One such prediction is that if the selective pressures of good genes and sensory exploitation are both strong and aligned, the response is firmly anchored by a double attraction in the upper area of the diamond. This means that the response should be extra-vulnerable to exploitation by another signaler such as a predator. At least Trinidadian guppies seem to abide to this rule. In that species, orangespotted males attract females and this attraction is maintained both by good genes (carotenoids are expensive) and sensory exploitation (a favorite nutritious food item is orange). In response, prawns evolved orange-spotted pinchers to lure them. For cultural evolution, perhaps similar predictions could be derived. For example, driving a motor vehicle is something that seems inherently pleasurable to many, which is likely on account of the fact that it effectively pushes a number of pre-existing 'pleasure-buttons' of evolved psychology. At the same time, it is conceivable that using motor vehicles also confers evolutionary benefits, for instance as a result of increased mobility. This double attraction may have caused motor vehicles to have become a widespread and stably appearing part of the culturally constructed niche of human populations around the globe. The pleasure buttons pushed by motor vehicle use should therefore also be vulnerable to exploitation. One such pleasure button may be the "need for speed," which is especially sensitive in male adolescents. A whole market segment depends on it, as manufacturers benefit from producing ever faster cars, preying on adolescents with hypersensitive need for speed. Exploitation seems at a cost to these individuals, in terms of spending lots of money on something many of them cannot afford and in terms of death before reproducing.[27] Thus, the model may allow to make predictions about processes linked to sexual selection and cultural evolution. Of course, it may be further fine-tuned or adjusted.

Studying the function(s) of art-appreciation through the psychological underpinnings of expert-judgments

Sometimes a distinction is made between high and low art. However, it is unclear whether this reflects mere snobbery, or whether there is something more going on. The studies in Chapter 8 probably help to get a grip on part of this issue. The studies indicate that in a visual art context, experts tend to have a 'negative' content bias (i.e., they preferred neutrally attractive faces more than attractive faces whereas laypersons preferred attractive faces). Remarkably, similar patterns have been found for wine expertise, e.g., opposite preferences of amateurs and connoisseurs (Goldstein et al., 2008; see Introduction), suggesting a more fundamental process in preference evolution. Yet, Chapter 8 left largely unexplored what the bio-cultural function(s) of art expertise and its reliance on this negative content bias can be. Here I present some thoughts on how the framework developed in this dissertation can assist in tackling this issue. My research (chapter 8) already indicates that art does not merely evolve to match preferences of evolved psychology, but prestige bias creates evolutionary dynamics that move art and its appreciation away from such preferences. Explaining these dynamics has implications for philosophy of art and aesthetics (e.g., it provides a tentative explanation for the fact that beauty and pleasure lost their central position in Western (high) art). More specifically, our research has shown that prestige bias trumps content bias among art experts but not among laypersons. Laypeople's appreciation of artwork (i.e., portraits) is positively affected by a content bias for attractive faces, mediated by aesthetic pleasure,

[27] The Global Status Report on Road Safety 2013 indicates that speeding is a key risk factor in traffic, that young adults aged between 15 and 44 years account for 59% of global road traffic deaths and that 77% of road deaths are among men. According to the World Health Organization, road traffic injuries caused an estimated 1.24 million deaths worldwide in the year 2010.

whereas experts' appreciation is positively affected by prestige and mediated by admiration for the artist. Moreover, experts confer lower appreciation to attractive compared to moderately attractive content. Recent empirical aesthetics research showed that compared to laypersons, experts exhibit attenuated emotional responses to content features of artwork and they like negative content more. But how exactly does one move away from content bias? What are associated proximate mechanisms and potential (ultimate) functions of this negative content-content bias? I believe that these questions can be – at least partially - answered with the help of experimental studies. Here, three possible functions of the negative content bias are sketched, together with (a set of) experimental studies that can help to assess whether these proposed functions apply.

Art as a cognitive challenge.

A potential mechanism of expert appreciation is that it is driven by a preference for neutrally attractive content. Neutrally attractive content, being less immediately rewarding than attractive content, may be more thought-provoking, eliciting questions regarding the artist's intentions. The cognitively oriented learning attitude of experts may drive them to thought-provoking stimuli in the art domain. This mechanism might serve the function of learning "better-than-average" information from artwork and artists: because of this preference for neutrally attractive content, the expert is more intellectually challenged[28] than the layperson with his preference for easy-to-like art.

A first set of experimental studies to test this hypothesis, represents a variation on the studies that we reported on in the previous chapter (Chapter 8). It replicates our previous study on art appreciation but adds physiological measures. Thus, art expertise, self-reported art appreciation, aesthetic pleasure and admiration for the artist would be complemented with implicit physiological measures (e.g., facial electromyography); content will be manipulated within and prestige between participants. We will examine whether we find the same pattern as in our previous studies[29]. The design implies 2x2 possible outcomes (association self-report & physiology with regard to neutrally attractive content; association self-report & physiology with regard to attractive content;dissociation self-report & physiology w.r.t.

[28] Maybe, it is better to see this as an example of the expert actively seeking for intellectual challenges. If this is the more accurate rendering, the bias can be seen as an example of what is guided variation.
[29] i.e., that experts confer higher appreciations to artwork depicting neutrally attractive content than to attractive content.

neutrally attractive content; dissociation self-report & physiology w.r.t. attractive content). Now, an association between self-reported appreciation and physiological measures of liking regarding neutrally attractive content depicted in artwork, would suggest that experts unambivalently prefer neutrally attractive thought-provoking content. This would correspond to the function of learning from art and artists (and eventually distinctiveness). Moreover, a positive association between the physiological response and prestige would indicate a stable prestige biased social learning motive in the art context and thus further support the learning function. A second study can assess functionality by manipulating potentially functional contexts of expert art appreciation and verifying to which of these manipulations explicit expert art appreciation is sensitive (cultural evolution and social psychology part). Whether expert art appreciation serves a learning function can then be analysed by manipulating curiosity (as in Weckx, Bruyneel, & Dewitte, under review). If increased curiosity would lead to a greater preference for neutral content, this would offer further support for the cognitive challenge-hypothesis.

The social affiliation of art experts.

Philosophers and sociologists have hinted at the idea that art appreciation should be understood as a badge of group membership. On this view, expertise primarily distinguishes experts from laypersons. After all, being an expert may not make much sense if expert appreciation does not differ from that of laypersons. This process may differentiate experts from laypersons and lends them a higher status. At the same time, it also unites experts, facilitating the defense of their common interests. Now suppose that the experimental studies show a dissociation between self-reported appreciation and physiological measures of liking regarding beautiful content depicted in artwork: the physiological response on beautiful content is stronger than on neutral content, whereas the self-report indicates the opposite. This would suggest that experts do experience pleasure as a result of stimulation of the evolved aesthetic preferences they share with laypersons, but they deliberately choose to ignore that (this corresponds to a uphill-battle process). This dissociation may correspond to group membership function. Second, group membership function is checked by manipulating the need to belong (Baumeister & Leary, 1995). We may the 'odd ball' paradigm, where people play a game with two virtual others (throwing virtual balls) where the virtual others gradually start excluding the participant and throwing only at each other. The social affiliation hypothesis predicts that increasing the need to belong will increase the differences between experts and laypersons, which may manifest itself in experts' higher rating for the neutral content art stimuli or a reduced rating for the attractive content art stimuli.

Art vs. Cheesecake: Avoiding exploitation through art expertise

It has been suggested that art is a type of pleasure technology that succeeds by exploiting individual's evolved aesthetic preferences. As such, spectators may trade off rewards from indulging in art and biological activities, resulting in less effort being allocated to reproduction. In the previous chapter (Chapter 8), we speculated that, as a consequence, art experts and other individuals who have been exposed to 'high doses' of art, may have socially learned to resist exploitation. As prestige bias may trump content biases, experts could achieve this by selectively preferring art from prestigious artists. Hence, the mechanism of preferring art from prestigious artists may serve the function of avoidance of fitness costs (e.g., opportunity costs, costs due to interference with the proper function of the evolved preferences). A dissociation between self-reported appreciation and physiological measures of liking regarding beautiful content depicted in artwork supports the social affiliation-hypothesis, but can also be reconciled with avoidance of exploitation. To specifically assess the avoidance of exploitation-hypothesis, one can conduct studies in which opportunity cost threat are manipulated, for instance by raising the effort required to watch the art. Respondents will see the picture for two seconds (which allows them to rate them) and have the opportunity to prolong the viewing time by exerting much or little effort (pressing the space bar at a high or low speed; Jaensch et al., 2014). The resistance hypothesis predicts that experts will be more sensitive to the effort they have to exert to view art with attractive content than a neutral content (compared to laypersons). Furthermore, if experts rely on prestige to counter exploitation, increasing exploitation threat may increase physiological response associated with prestige.

Conclusion

Existing accounts of the evolution of the arts are most often conceptualized within the framework of standard evolutionary psychology. Within this framework, culture is regarded as either an extension of genes or as something that should be left out of the evolutionary equation (i.e., a mere byproduct of evolution). However, throughout this thesis I argued that these accounts are often simplified to the point of distortion and made the case for a more expansive *cultural* evolutionary approach that considers culture as something that can evolve partly independently from genetic evolution. This framework also permits to formulate and explore a number of novel hypotheses about the arts. In the final chapter of this dissertation, we developed and experimentally verified a few of such hypotheses, based on prestige biased social learning theory, in an attempt to contribute to explaining differences between high art and popular art and their appreciation. Furthermore, in the section above, I proposed ways in which this experimental research could be continued and further elaborated. I hope that this dissertation could convince its reader that future research into the evolution of the arts could benefit from this more comprehensive and more fine-grained evolutionary framework.

References

Goldstein, R., Almenberg, J., Dreber, A., Emerson, J. W., Herschkowitsch, A., & Katz, J. (2008). Do More Expensive Wines Taste Better? Evidence from a Large Sample of Blind Tastings. *Journal of Wine Economics*, *3*(1), 1–9. doi:10.1017/S1931436100000523

Jaensch, M., van den Hurk, W., Dzhelyova, M., Hahn, A. C., Perrett, D. I., Richards, A., & Smith, M. L. (2014). Don’t Look Back in Anger: The Rewarding Value of a Female Face Is Discounted by an Angry Expression. Journal of Experimental Psychology: Human Perception and Performance. Advance online

Weckx, L.; Bruyneel, S.; & Dewitte, S. (under review). Incidental Curiosity Increases Consumption of Unrelated Information in Domains of Expertise.

Appendices

Appendix 1: When Art Imitates Life: Universal Aesthetic Preferences For Natural Elements And Their Evolutionary Origins (Chapter In Monograph On The Artist Ahae)

Introduction

This essay discusses empirical research indicating that humans possess default aesthetic preferences for natural elements. There are reasons to believe that these preferences are at least partially innate and stem from selective pressures that consistently occurred in our evolutionary past. The aim of this essay is not to formulate an opinion on the aesthetic value of Ahae's work on the basis of these scientific findings and theories. Rather, I will attempt to show that Ahae's artistic choices are very much in line with the aesthetic preferences evolutionary aesthetics claims modern humans have inherited from their forebears. In light of this body of scientific work it seems that Ahae's art explores a realm of spontaneous and direct aesthetics, which is often neglected in current postmodern times (cf. Knížák, 2011).

The Landscape

Empirical research over the last two decades showed that humans across cultures and continents have strikingly similar preferences for landscapes and artistic representations thereof. One such study was conducted in 1993 by the artists Vitaly Komar and Alexander Melamid. They organized a worldwide poll which allowed them to assess the artistic preferences of close to two billion people spread over ten countries. They found that almost without exception, people around the world gravitate toward the same general type of pictorial representation: a landscape with trees and open areas, water, human figures, and animals. Other empirical studies yielded similar findings.

Adherents of "evolutionary aesthetics" believe that the universality of human landscape preferences appeal to an evolutionary explanation: rather than being the product of recent enculturations they may in fact be innate preferences that were selected for in our ancestors. Evolutionary psychologist Thornhill (2003, p 9) summarizes how evolutionary aesthetics is commonly understood by its proponents. He states that "[b]eauty experiences are unconsciously realized avenues to high fitness in human evolutionary history. … The Darwinian theory of human aesthetic value is that beauty is a promise of function in the environments in which humans evolved, i.e., of high likelihood of survival and reproductive success in the environments of human evolutionary history. Ugliness is the promise of low survival and reproductive failure. Human aesthetic value is a scale of reproductive success and failure in human evolutionary history, …" Thus, in short, evolutionary aestheticians explain beauty experience and aesthetic appreciation in terms of fitness maximization. Founder of sociobiology Edward O. Wilson (1984) coined the term "biophilia" to describe the innately emotional affiliation of human beings to natural phenomena such as animals, plants and habitats. Wilson (1984) emphasized that aesthetic judgments are central to biophilia.

One branch of evolutionary aesthetics specifically applies this evolutionary reasoning to explain landscape and landform preferences. "Habitat theory" which was originally proposed by environmental psychologists Orians and Heerwagen (1992) is the assumption that humans have "inborn" (aesthetic) preferential biases for particular landscape features and/or organizations, and elements that were invariably present in ancestral environments (e.g., animal-life, water features). Preferential biases for these features/organizations and elements are claimed to be evolved adaptations. They increased genetic fitness by enhancing the probability that ancestral humans would explore environments which offered them sufficient opportunities for protection (e.g., against predators, weather) and which guaranteed the availability of resources.

Within this context, Orians and Heerwagen (1992) put forward a general account of the kind of ideal landscape that human beings would find intrinsically pleasurable. This landscape has much in common with the savannas and woodlands of East Africa where the last common ancestors of humans and chimpanzees lived and where much of early human evolution occurred; hence it is called "the Savanna Hypothesis." Among other characteristics, the landscape type envisioned typically includes open spaces with fairly even ground surfaces covered with grasses, interspersed with thickets of bushes and groupings of trees; an unimpeded vantage on the horizon; the presence of water directly in view or evidence of water nearby; evidence of animal life included birds; and a diversity of greenery (Orians & Heerwagen, 1992; Ulrich, 1983). An evolved (aesthetic) preferential bias for environmental features or configurations typical to this biome made that early humans were drawn to environments where potential dangers (e.g., predators) could be seen from quite a distance and where locomotion was relatively easy and unimpeded. Moreover, to our meat-eating forebears, this type of habitat contained more protein per square mile than any other landscape type.

A closely related hypothesis, originally proposed by Appleton (1975), states that a fundamental element in the attractiveness of a landscape is whether it affords the ability to "see without being seen." Human beings like a prospect from which they can survey a landscape and at the same time they enjoy a sense of refuge. A cave on the side of a mountain, a house on a hill, or "*a room with a view"* count as situations with appeal (Dutton 2009, p 21). People prefer places that have an overhang of some sort, such as a roof, along with a sense of being safe from observation or attack from behind.

Philosopher of art Dennis Dutton (2009) notes that, in line with the prospect-refuge hypothesis, most landscape representation in the history of painting places the implied viewer either at some desirable vantage point or, if at ground level, at a somewhat greater height than what would be accurate for a six-foot human being. Ahae's *Through My Window* collection of photographs appeals to virtually all of the aesthetic preferences just described. He operates from a safe viewpoint that enables him to survey the landscape and from which he portrays a scenery that exhibits nearly all of the elements of Orians and Heerwagen's (1992) ideal landscape. The photographs show open spaces, diversity of greenery, groups of trees, presence of water, a vantage on the horizon, and animals observed from Ahae's vantage point. Interestingly, whenever Ahae focuses on specific details in the scenery in his close-up images, he turns to the subjects which are predicted by evolutionary aesthetics to elicit attention and exploration more than anything else: animal and vegetative life.

Animal and vegetative life

The elements that have been invariably present across the range of possible habitats human ancestors have inhabited (in addition to the savanna), and that were especially relevant to their survival, seem above all to pertain to the category of "living things", specifically animals (including conspecifics) and vegetative life. It is a truism that during human evolution negotiating successfully with animals – either being predator or prey – as well as the ability to locate and gather foods of vegetal origin (e.g., roots, flowers, berries, herbs), were of crucial importance to human survival. Given these selective pressures, it has been claimed that humans evolved a number of (affectively guided) detection, recognition and memory mechanisms

(Barrett, 2005). Consistent with this, experimental research supports the claim for the existence of domain-specific cognitive (i.e., attentional, memory) and emotional mechanisms to deal with the category of living things. For example, children are already at very young age able to make a differentiation between (crucial features differentiating) animate and non-animate categories (Gelman & Opfer, 2002). Neuropsychological research into so-called "category specific deficits" points to the existence of domain specific neural areas that are specialized in storing knowledge about living/animate entities (e.g., animals, vegetative life) (Caramazza & Shelton, 1998).

Regarding the category plant life females seem to have a number of cognitive advantages over males, possibly reflecting an evolved/ancient division of labor (i.e., females as gatherers, males as hunters). For example, Neave and colleagues (2005) found that females are quicker than males in recognizing plant targets and in remembering the location of those targets (for similar results, see: Schussler & Olzak, 2008). Research also indicates a female, as opposed to a male advantage for location memory for fruits (New, Krasnow et al., 2007; Krasnow, Truxaw et al., 2011). Data from semantic knowledge studies point out that females have an advantage to males for knowledge about plant categories (Laiacona, Barbarotto & Capitani, 2006).

With regard to animal-life it has been shown that neurons in the right amygdala respond preferentially to pictures of animals, which might reflect the evolutionary significance of this category of animates (Mormann et al., 2011). Pratt and colleagues (2010) found that animate motion captures visual attention more readily than inanimate motion. New, Cosmides and Tooby (2007) report that respondents are faster and more accurate in detecting changes to scenes containing animals than to scenes with inanimate objects, such as vehicles. Eye-movement studies show that respondents are more likely to attend to animals than to objects, and animals are also attended longer time than objects (Yang et al., 2012). In a real life setting (window displays in a mal), the presence of animal-life is found to lead to increased attention and exploration (Windhager et al., 2011). Of further importance is that lesion studies show that males are more likely to become impaired for knowledge about plant life than about animals. Scotti, Laiacona and Capitani (2010) argue that other factors than familiarity need to be taken into account to explain this animal advantage. Specifically, they speculate that this pattern reflects males' role as hunters in ancestral times.

The adaptive human fascination with animals and plant motives is reflected by its presence in art across times and cultures (e.g., Verpooten & Nelissen, 2010 (Chapter 7); Joye 2006). Especially nonhuman animals are among the most dominant themes in the visual arts, even before historical times. On decorated rocks and in prehistoric cave walls in Europe animals constitute by far the most often depicted figurative representations, especially large wild animals, such as bison, horses, aurochs, and deer.

Conclusions

In this essay I have shown that the artistic themes of Ahae's *Through My Window* collection of photographs correspond to default aesthetic preferences of humans. One currently influential explanation links these aesthetic preferences to human evolution: evolutionary aesthetics predicts that the experience of beauty holds the promise of function in the environments in which humans evolved, i.e., of high likelihood of survival and reproductive success in the environments of human evolutionary history. The theory states that we have retained these aesthetic preferences from our ancestral past. An artist may choose to tap into these preferences in order to elicit fluent and direct aesthetic experiences. It seems reasonable that such aesthetic experiences stimulate to seek a renewed connection with our natural environment. Some aspects of Ahae's work may be designed to appeal to these aesthetic preferences in order to achieve exactly this.

References

Appleton, J. (1975). *The experience of landscape*. New York: Wiley.

Barrett, H.C. (2005). Adaptations to predators and prey. In D.M. Buss (Ed.), *The Handbook of Evolutionary Psychology* (pp. 200–223). New York: Wiley.

Caramazza, A., & Shelton, J. R. (1998). Domain-specific knowledge systems in the brain: The animate-inanimate distinction. *Journal of Cognitive Neuroscience, 10*, 1–34.

Dutton, D. (2009). *The art instinct: Beauty, pleasure and human evolution*. Oxford: Oxford University Press.

Gelman, S.A., & Opfer, J E. (2002). Development of the animate-inanimate distinction. In U. Goswami (Ed.), *Blackwell Handbook of Childhood Cognitive Development* (pp. 151 - 166). Oxford, UK: Blackwell.

Joye, Y. (2006). Evolutionary and cognitive speculations for biomorphic architecture. *Leonardo Journal of Sciences, 39* (2), 145-152.

Krasnow, M.M., Truxaw, D., Gaulin, S.J., New, J., Ozono, H., & Uono, S., et al (2011). Cognitive adaptations for gathering-related navigation in humans. *Evolution and Human Behavior, 32*, 1–12.

Laiacona, M., Barbarotto, R., & Capitani, E. (2006). Human evolution and the brain representation of semantic knowledge: Is there a role for sex differences? *Evolution and Human Behavior, 27*, 158-168.

Mormann, F., Dubois, J., Kornblith, S., Milosavljevic, M., Cerf, M., & Ison, M. et al. (2011). A category-specific response to animals in the right human amygdala. *Nature Neuroscience, 14*, 1247–1249

Neave, N., Hamilton, C., Hutton, L., Tildesley, N., & Pickering, A. (2005). Some evidence of a female advantage in object location memory using ecologically valid stimuli. *Human Nature, 16*, 146–163.

New, J., Cosmides, L., & Tooby, J. (2007). Category-specific attention for animals reflects ancestral priorities, not expertise. *Proceedings of the National Academy of Sciences, 104*, 16598–16603

New, J., Krasnow, M.M., Truxaw, D., & Gaulin, S.J. (2007). Spatial adaptations for plant foraging: Women excel and calories count. *Proceedings of the Royal Society B: Biological Sciences, 274*, 2679–2684

Orians, G.H., & Heerwagen, J.H. (1992). Evolved responses to landscapes. In J.H. Barkow, L. Cosmides & J. Tooby (Eds.), *The adapted mind. Evolutionary psychology and the generation of culture* (pp.555–579). New York: Oxford University Press.

Pratt, J., Radulescu, P., Guo, R.M., & Abrams, R.A. (2010). It's alive! Animate motion captures visual attention. *Psychological Science, 21*, 1724-1730.

Schussler, E.E., & Olzak, L.A. (2008). It's not easy being green: student recall of plant and animal images. *Journal of Biological Education, 42*, 112–118.

Scotti, S., Laiacona, M., & Capitani, E. (2010). Brain damage and semantic category dissociations: is the animals category easier for males? *Neurological Sciences, 31*, 483-489.

Thornhill R (2003) Darwinian aesthetics informs traditional aesthetics. Pp. 9-38 in *Evolutionary Aesthetics*, K. Grammer and E. Voland, eds. Springer-Verlag, Berlin, Germany.

Ulrich, R.S. (1983). Aesthetic and affective response to natural environment. In I. Altman & J.F. Wohlwill (Eds.), *Human behavior and the environment: Volume 6* (pp. 85–125). New York: Plenum Press.

Verpooten J., Nelissen M. (2010). Sensory exploitation and cultural transmission: the late emergence of iconic representations in human evolution. *Theory in Biosciences, 129*, 211 – 221.

Wilson, E. O. (1984). *Biophilia.* Cambridge: Harvard University Press.

Windhager, S., Atzwanger, K., Bookstein, F.L., & Schaefer, K. (2011). Fish in a mall aquarium—An ethological investigation of biophilia. *Landscape and Urban Planning, 99*, 23-30.

Yang, J., Wang, A., Yan, M., Zhu, Z., Chen, C., & Wang, Y. (2012). Distinct Processing for Pictures of Animals and Objects: Evidence From Eye Movements. *Emotion*. Advance online publication. doi: 10.1037/a0026848

Appendix 2: Sensory Exploitation: Underestimated In The Evolution Of Art As Once In Sexual Selection Theory?

Introduction

Before addressing the question of the evolution of art it may be useful to consider another question first: what is art? This question has no agreed-upon answer. Some philosophers of art even claim that art is intrinsically indefinable (e.g., Gaut 2005). Others devote their careers trying to define art (see for a summary: Adajian 2007). Definitions or rather descriptions of art seem to be extremely dependent on the perspective of the (sub)discipline from which they are undertaken, and the works of art that are considered relevant by researchers; for example, video games are seldom considered art today, but probably will be by a new generation. Maybe it is because the term "art" traditionally denotes something of value or significance (comparable to the impact of the label "scientific") that people never seem to stop discussing what is art and what is not. Some – especially artists – will claim art to be indefinable, thus contributing to its charm and appeal.

However, when considering art from an evolutionary perspective we *need* some sort of a description of art to work with, and a rather general one, since evolutionary theory — as a scientific theory — is about general processes. In most approaches of natural scientists art is described as "aesthetically pleasing" (e.g., Dissanayake 1992; Miller 2000, 2001; Ramachandran and Hirstein 1999; Pinker 1997, 2002), but this is arguably a too narrow description of art. Meaning (symbolic, in the sense of referring to something outside the work of art) is also important in art, and is usually not reducible to aesthetic appeal, if the work of art is meant to be aesthetically pleasing at all. So, our general description should ideally cover such disparate examples as placing a *urinoir* entitled "Fountain" in an exhibition space, the extremely popular and extremely violent video game Grand Theft Auto, and a tradition of weaving ornamental baskets. Van Damme (2008, p. 30) writes: "Numerous contemporary definitions of the term "art" mention in one way or another both "aesthetics" (denoting say, high quality or captivating visual appearance) and "meaning" (referring to some high quality or captivating referential content) as diagnostic features, although any clear-cut distinction between the two appears unwarranted, if only since there is no signified without a signifier." Furthermore, we will consider art as a signaling *behavior*, following Dissanayake's (1992, p. 8) ethological approach: "a 'behavior of art' should comprise both making and experiencing art, just as aggressive behavior presupposes both offense and defense." Thus, here we view "artistic behavior" as producing and experiencing "signals" (or a perceivable object emitting signals) with captivating meaning and/or form (design) to group members.[30]

The concept outlined in this chapter takes all this into account and is based on a biological model of signal evolution, namely Sensory Exploitation (SE). SE is a fairly recent model that is currently gaining field in sexual selection theory, where it offers a refreshing alternative to the classic perspective on the evolution of signal sending and receiving in courtship behavior. We argue that it should do the same for the evolution of human artistic behavior. SE deserves more attention in evolutionary thinking about art than it has received until now. To avoid any misunderstandings we would like to stress that using a model from sexual selection to address questions about the evolution of human artistic behavior does not in any way imply (or exclude) that art evolved as a sexual display. How this works will be explained below.

Many proposals about the evolution of art have been based on or linked to sexual selection in one way or another (e.g., Low 1979; Eibl-Eibesfeldt 1989a, 1989b). The first ideas in this direction came, as so often in evolutionary biology, from Darwin himself. They can be found in his second book on evolution in which he covered both sexual selection and "the descent of man" (Darwin 1871). For example, Darwin suggested that bird song and human proto-song, which he thought would have been especially exerted during the courtship of the sexes, were evolutionary analogues. He even posited that some animals possessed a "sense of beauty" quite similar to ours and that this capacity had significant evolutionary consequences (Darwin 1871, p. 301): "When we behold a male bird elaborately displaying his graceful plumes or splendid colors before the female, whilst other birds, not thus decorated, make no such display, it is impossible to doubt that she admires the beauty of her male partner." Put differently, Darwin was the first to postulate that elaborate male display traits (such as ornament, song, and dance)[31] have evolved by appealing to

[30] Although art may also be "captivating" to other groups of the same species or even to other species on earth or elsewhere, this is not necessarily so. Moreover we will argue art evolved *because* it is captivating to group members (and to artists themselves).

[31] Often a distinction is useful in mating behavior between intersexual signaling and intrasexual competition for mates. While peacocks use their tails to court peahens, antlers and other "weapons" are used to fight same-sex rivals.

choosy females' senses. The idea that a sense of beauty would have evolutionary consequences is obviously inspiring in relation to questions about the evolution of aesthetic signals and art. (The above-mentioned concern that art is not only about beauty does not devalue the general principle of Darwin's hypothesis, provided that sexual selection is perceived from the SE perspective.)

We will review and evaluate two existing applications of sexual selection to the evolution of art, borrowing ideas and contrasting our view with them. In order to do this, a preliminary discussion of current models of sexual selection is required. In the second section we discuss two types of sexual selection models that address the evolution of male display traits and female preferences. There is the indirect benefit model in which females develop preferences for certain male traits that are adaptive (or indicators thereof). These preferences are indirectly selected for in the course of evolution, because the good choices (for males with adaptive traits) are rewarded with fitter offspring (since they inherited both the genes for good choice and the adaptive traits, which they pass on to their sons and daughters). This circular process can run out of hand. Since genes for good choice and genes for adaptive traits become genetically correlated (meaning they are passed on together to the next generations), they can be caught in a potentially maladaptive runaway process. It is basically this indirect benefit model that has been used by both Miller (1998, 1999, 2000, 2001) and Boyd and Richerson (1985, ch. 8) to address the evolution of aesthetic displays and art in humans. Miller proposes that art may in fact quite literally have evolved as a sexual display through indirect benefit processes on the genetic level. Boyd and Richerson (1985, ch. 8) focus specifically on the explanatory possibilities of the runaway process. They apply the model to cultural level processes, thus using a sexual selection model to postulate a non-sexual,[32] cultural runaway process that leads to the spread of cultural aesthetic traits. These two hypotheses are reviewed and discussed in the first part of the third section.

The other sexual selection model discussed in section 2 is SE. From the SE perspective, female preferences are sensory biases that have originated in another context than the current mating context and that may be maintained by the utility they have in that context (e.g., finding food). A male evolves display traits that exploit these female sensory biases, since captivating the female's attention or just plainly misleading her (e.g., by mimicking food) increases his reproductive success. We conclude section 2 with summarizing why

---

Here we focus on the former.

[32] Cultural variants as analogues to genes are also passed on through reproduction, but not through sexual reproduction; however, they are reproduced through imitation and other forms of social learning.

this alternative (or at least addition) to the classic indirect benefit model is important in sexual selection theory. In the second part of section 3, SE is applied to human artistic behavior as an addition or even alternative to the existing hypotheses. So here we argue that art evolved by exploiting human biases for certain meanings as well as design or formal aspects. Animal biases that are exploited can be quite complex, determined not only by innate dispositions or engineering details of the sensory system of the signal receiver but also by psychological factors such as emotions and (social) learning (e.g., Guilford and Dawkins 1991) and we can expect the same for human biases. To the person who experiences a work of art there might be no direct utility involved, just as the female that is misled by the male mimicking food may not benefit from being sensorily fooled. SE is typically applied to sexual selection cases in which the traits or signals exploiting biases are genetically encoded male display traits (e.g., orange spots resembling food in guppies). However, borrowing from Boyd and Richerson's (1985, ch. 8) model, sensory exploitation also applies to non-sexual contexts, and exploiting signals may be culturally transmitted as well. So, SE does not need to imply that art evolved through courtship. Here we are not specifically interested in the reproductive success of the artists, but in the reproductive success of artistic signals themselves that spread through cultural transmission regardless of beneficial effects to individuals that transmit them, just as male ornaments evolve through sensory exploitation without the need of any benefits to females. This possibility of non-functional evolution of art will be a theme throughout this chapter. We will mainly focus on iconic representations and also briefly discuss "self-exploitation" and make a sketchy comparison of art and religion in relation to human mental biases. In section 4, we summarize our evaluation and articulation of existing hypotheses based on the SE view on art.

Sexual selection theory

To make our argument it is not necessary to provide a full overview of sexual selection theory. We will only focus on those models applicable to the evolution of art. These are the indirect benefit or "Fisher-Zahavi model" (Eshel et al. 2000; Kokko et al. 2003) and SE (e.g. Ryan 1990, 1998). Both Boyd and Richerson and Miller use the former; our concept is based on the latter.

Mate choice is an important evolutionary process that imposes sexual selection on the other sex and accounts for spectacular traits and behaviors that would otherwise remain unexplained by natural selection (Darwin 1871; Andersson 1994). Both the indirect-benefit model and SE describe the relation between mate choice and these traits and behaviors. For an insightful review of sexual selection models in general — much in this section is based on it — see Kokko et al. (2003).

Indirect-benefit model

The Fisher-Zahavi model is an indirect-benefit model of mate choice. Both the so-called good genes selection hypothesis (or fitness indicator theory) and Fisher's runaway process fall within this category. The good genes selection hypothesis simply states that females choose partners based on indicators of genetic quality. The evolutionary logic behind this behavior is that they as such provide their offspring with good genes. Choosing good genes positively influences the viability of the offspring and increases the chances that the female's offspring reaches reproductive age. So female choice for indicator traits is indirectly selected by piggybacking on the directly naturally selected good genes (Fisher 1930, formally demonstrated by Lande 1981). Closely related to the good genes hypothesis is the handicap principle. It predicts the game-theoretic constraint that indicators must be costly to be reliable because if not they can be faked too easily (Zahavi 1975, 1991; Zahavi and Zahavi 1997).

Thus, fitter males, and the females who preferentially mate with them, will have offspring that inherit the genes for both fitness and the mating preference. The resulting linkage disequilibrium [33] between preference genes and male fitness favors the spread and elaboration of the preference by indirect selection. Fisher's insight, that the increased importance of attractiveness as a component of male fitness can drive the exaggeration of a male trait signaling fitness beyond its otherwise naturally selected optimum, is known as the "Fisherian runaway" process. So long as the process is unchecked by severe counterselection (i.e., survival costs), it will advance with ever-increasing speed (Fisher 1930).

Sensory Exploitation

Selection operating directly on the psychosensory system in contexts other than mate choice may either maintain or drive changes in mating biases (Williams 1966; Sober 1984; West-Eberhard 1984, 1992; Ryan 1990, 1995, 1998; Ryan and Rand 1990, 1993; Ryan and Keddy-Hector 1992; Endler 1992; Arak and Enquist 1993, 1995; Shaw 1995; Dawkins and Guilford 1996; Endler and Basolo 1998; Autumn et al. 2002). To some extent mate choice may thus evolve by a process variously known as SE (e.g., Ryan 1990, 1998), sensory drive (e.g., Endler 1992), pre-existing bias, or sensory trap (e.g., Christy 1995). For example, across some

---

[33] In population genetics, linkage disequilibrium is the non-random association of genes at two or more loci. In this specific case it means that the "gene" for preference for certain male display traits becomes correlated to the "gene" for the male display trait itself, since both genes are inherited by offspring. In sons the gene for the preference trait is not expressed, but it is in the sons' daughters, and vice versa, the gene for the display trait is not expressed in the daughters but it is in the daughters' sons.

populations of guppies the strength of attraction to orange objects in a non-mating context explains 94% of the inter-population variation in female mating preferences for orange male ornaments (Rodd et al. 2002). This means that in populations where females are strongly attracted to orange food items, they will also tend to choose males mimicking these orange food items; hence, the reproductive success of males that happen to have orange spots in these populations increases and over a certain number of generations these orange spots may become ever more accurate mimics[34] of orange food items. Thus female sensitivity to orange-colored food items may be at least as important to the evolution of female mating preferences for males with large orange spots as any direct and indirect benefits that more-orange males deliver to their mates. SE may do more than offer a quirky exaptive[35] alternative for how mating biases and male display traits evolve. Whenever studying a biological trait within the Darwinian framework it is important to distinguish between the selective forces that led to its origin, its evolution, and the processes that maintain it (Fisher 1930). The origin of mating biases and displays are relatively hard to explain with the indirect-benefit model (Arnqvist 2006). SE, however, may provide the initial "nudge" often required initiating choice-display coevolution (Arak and Enquist 1995; Payne and Pagel 2000). Recent empirical research and theoretical models suggest that origin by SE has been widespread (Rodriguez and Snedden, 2004; Arnqvist 2006). And maybe choice-display coevolution is not even required to explain the evolution of male ornaments, as we will discuss below.

Arnqvist (2006) distinguishes two classes of origins of sensory biases. Firstly, females are adapted to respond in particular ways to a range of stimuli in order to, for example, successfully find food, avoid becoming food for predators and breed at optimal rates, times, and places. Such multi-dimensional response repertoires form a virtually infinite number of pre-existing sensory biases that are potential targets for novel male traits. These he names "adaptive sensory biases." Notice that male traits that result from exploiting these adaptive sensory biases are in fact mimics. Secondly, pre-existing sensory biases need not be the direct result of selection. In theory, they can simply be incidental and selectively neutral consequences of how organisms are built (Ryan 1990; Endler and Basolo 1998). For example, artificial neural network models have shown that networks trained to recognize certain stimuli seem to generally

---

[34] The term "mimic" usually refers to a whole, mimicking organism (e.g., Pasteur 1982), but as Maran (2007, p. 237) usefully points out, from a semioticist viewpoint "neither the mimic nor the model needs to be a whole organism but can be just a part of an organism both in spatial or temporal terms or just a perceptible feature." So here we use mimic in the latter sense.
[35] An exaptation is a pre-existing trait that acquires a new beneficial effect without modification to the phenotype by selection (Gould, 1991).

produce various sensory biases for novel stimuli as a byproduct (Enquist and Arak 1993, 1994; Arak and Enquist 1993; Johnstone 1994). Similarly, research in "receiver psychology" (e.g. Guilford and Dawkins 1991; Ghirlanda and Enquist 2003) has also suggested that higher brain processes may incidentally produce pre-existing sensory biases for particular male traits. Following Arak and Enquist (1993), Arnqvist (2006) refers to such sensory biases as "hidden preferences". These, then, can be seen as side effects or contingencies of how the sensory system, defined in its widest sense, of the receiver is constructed. Usually it results in abstract biases, e.g., for symmetrical or exaggerated traits (Ryan 1998). Arnqvist's (2006) distinction is quite similar to the one mentioned above between "aesthetics" and "meaning", which is made in most contemporary definitions of art. In the next section we will exploit this similarity for constructing our SE concept of art.

All sensory systems have biases, and mating biases are therefore inevitable (Kirkpatrick and Ryan 1991; Arak and Enquist 1995). Of course, not all possible sensory biases are exploited in a mating context, although theoretically they could be. For example, Burley (1988) showed that female zebra finches prefer males whose legs have been experimentally decorated with red or black plastic bands, while males with blue and green bands were rejected. Basolo (1990) showed that female platyfish prefer males with colorful plastic "swords" glued on the ends of their tails, suggesting that this preference also pre-dated the evolution of such ornaments in their close relatives the swordtails. These could be called "latent" preferences (Miller 1998, 2000), preferences resulting from biases that are present but not exploited in a sexual context.

Sensory Exploitation versus indirect-benefit model?

The preceding discussion shows us how SE and indirect benefits are generally considered intimately intertwined in determining the evolution of female biases and male display traits. Thus Kokko et al. (2003) write: "Even when a male trait has evolved to exploit a pre-existing sensory bias, indirect selection on the female preference may occur owing to the benefits accruing from the production of more-attractive sons. Such a signal may potentially then become secondarily genetically correlated with other fitness-enhancing traits." So, Kokko et al. (2003) state here that even if SE happens, indirect selection will likely influence female mating preferences, which would in turn influence male display traits and so on, hence a runaway process. However, there is no theoretic reason to assume this would be a necessary outcome. Consider the example of the female preference for orange spots in male guppies again. The female preference for orange spots is in fact a preference for orange food and the preference for orange food is maintained by the fact that it is useful in food gathering. As a result, the mating preference for orange-spotted males can't be altered without selecting against something highly useful for food gathering. SE happens because of stabilizing selection[36] against changes to the preferences, which would have to be mediated by changes to the perceptual system that would be detrimental to the guppies in other ways (given the limited number of ways to get guppies to do what they need to do). In that sense, then, SE is sensitive to the problem of the evolution of female preferences, it's just that the guppies have the orange spot preferences they do because any other genuinely biologically possible preferences would be detrimental, not because orange spot preferences are linked to fitness in some further way. Moreover, Kokko et al. (2003)'s use of the concepts "fitness" and "indirect benefit" are misleading. It can mean: good genes for survival *and/or* good genes for acquiring mates (attractiveness). Kokko et al. (2003) suggest the evolution of male display traits such as orange spots could be mediated by indirect benefits. But do they supply good genes for survival or are they just indicative of sexy son genes? It is quite possible that having orange spots does not correlate at all with genetic quality for viability. In that case, orange spots cannot and will not be selected as indicators of good genes for survival. These are important observations because they imply the possibility that evolution of male display traits may have more to do with the mechanism of SE than with indirect selected traits such as female preferences for indicators of genetic quality for viability (see Fuller et al. 2005). The strong version of SE can thus be perceived as an alternative to the indirect-benefit model in sexual selection and some researchers have offered it as such. At least some of the sensory biases and displays we find in nature might be the result of SE alone (West-Eberhard 1984; Ryan 1990, 1998). We stress this possibility because it will be central in our argument in the next section that the strong version of the SE concept might offer an alternative model for the evolution of art.

Biological mimicry

In some cases it is clear that good genes selection and runaway processes can never happen, but that nevertheless impressive ornaments evolve through signal evolution — that is in situations where benefits for the exploiter cannot in any way imply benefits for the signal-receiver. Some cases of biological mimicry fall within this category. For instance, in the genus *Ophrys*, plants evolved to attract male bees as pollinators by mimicking female mating signals. Here evolution by SE — the plants don't give any rewards

---

[36] Stabilizing selection, also referred to as purifying selection or ambidirectional selection, is a type of natural selection in which genetic diversity decreases as the population stabilizes on a particular trait value. Put another way, extreme values of the character are selected against. It is probably the most common mechanism of action for natural selection.

in return — seems to be the only possible explanation (Schiestl and Cozzolino 2008; Jersakova et al. 2006). Of course, in this example indirect genetic benefits don't apply because sensory biases of another species are exploited. But even intra-species SE in a sexual context may occur without good genes for viability selection, as the following example illustrates. Many cichlid fish species independently have evolved mouthbreeding as a highly specialized brood care behavior. Egg dummies, resembling the ova of the corresponding species, formed of various parts of the body can be found in different lineages of mouthbreeding cichlids. Most abundant are egg spots, which are conspicuously yellow spots on the anal fin of males. Females of mouthbreeding cichlids undoubtedly evolved sensory capabilities to detect eggs and are supposed to have a strong affinity for them, because they pick them up immediately after spawning. In fact, the ability to detect the eggs directly affects the female's fertility. Every missed egg results in a reduction in fitness. Consequently, a pre-existing sensory bias might have occurred in early mouthbreeders and might still occur in mouthbreeding species without egg dummies. As a consequence, males would have evolved egg spots in response to this sensory bias (Tobler 2006).

After the female (receiver) has picked up her eggs (model), the male displays in front of her, showing the egg spots on his anal fin (mimic). The female responds to the life-like egg illusion by a sucking reaction – and obtains a mouthful of sperm from the canny male in the process. One of us (Nelissen) has performed quite some research on cichlids and has described the system of the egg spots (in *Tropheus* and *Simochromis*). During courtship males vibrate their body while showing the egg spots to the female. It could well be that by doing this they enhance the egg illusion, giving it a more three-dimensional effect in combination with the light-dark grading in color and the colorless outer ring the egg spots exhibit (e.g., Wickler 1962). It may be that the female's mating preference for a male with well-elaborated egg spots does not yield in any direct benefits for the female, nor any good genes for viability of the female's offspring. Runaway selection is also limited by the mimicking function of the egg spots: they may need to remain life-like in order to mislead the female. As explained above, female preference for egg-like signals cannot be altered because of the functional importance of this preference outside the courtship context. Thus this might well be an example of the strong version of SE. The female's mating preference may be solely maintained by exploiting the benefit of the detection of eggs after spawning (Tobler 2006). Interesting to the problem of the evolution of human representational art is that cases of mimicry, such as this one, show how SE can produce two-dimensional representations (the egg spots) on a surface (the anal fin of the male) of three-dimensional objects (the eggs). In section 3.3.1. we will use this case as an example of SE in non-human animals and compare it to visual art in humans from a semiotic viewpoint.

Summary of section 2

SE is a crucial addition to or possibly even an alternative — at least under certain conditions — to the indirect-benefit model to explain the evolution of signals used in sexual contexts. Likewise, as we will argue in the next section, it also applies to the evolution of art. Here is a short summary:

- SE may provide the initial nudge for the evolution of male displays.
- SE may either maintain or drive changes in mating biases. As a result, male display traits may not necessarily be indicators of good genes for viability (i.e., survival).
- Cases of mimicry are clear-cut examples of the influence of SE as a mimic evolves to exploit sensory biases. Moreover, stabilizing selection on the female's sensory system inhibits changing its adaptive sensory biases by choice-display coevolution.

In section 3 we will show that a substantial portion of the discussion about the evolution of art is situated around the same questions as the ones covered in this section. We will thus use these summarized insights from this section to address them.

Hypotheses about art

Both Miller and Boyd and Richerson built their hypotheses upon the indirect-benefit model, although they do so in quite different ways. In particular, the framework in which they apply the indirect-benefit model differs. Both their hypotheses are Darwinian, but Boyd and Richerson formalize the influence of culture into their models while Miller's model focuses on genes. Both approach art from a signal evolution perspective: there is a signaler (the producer of art), and a set of receivers (who perceive or experience the work of art).

Miller's proposal

Being an evolutionary psychologist, Miller (2000, 2001) considers the capacity to produce and appreciate art as a "psychological adaptation": an evolved domain-specific mental capacity. Art as such serves a sexual function, as an extension, as Miller argues, of the human mind that itself evolved as a seducing device or an "entertainment system" by sexual selection (Miller 2000). In Miller's view human art making is exactly like bower building by male bowerbirds as follows. Females prefer to mate with males who construct larger, better quality, and more highly ornamented bowers (e.g., Borgia 1995). The bower can be considered as the “extended phenotype” of the male bowerbird (Dawkins 1982): a genetically evolved, species-specific artifact constructed outside the individual’s body, but very much in the service of the individual’s genes. Just like a bower, art is an aesthetic display that coevolved with aesthetic preferences (Miller 1998, 1999, 2000, 2001). It is an indicator of fitness. This means it is an indicator of reproductively important traits such as health, fertility, and genetic quality. “Perhaps beauty boils down to fitness” and “an art-work’s beauty reveals an artist’s virtuosity”, Miller (2001) states. Virtuosity, indicative of creative application of high skill and high intelligence, is such a fitness indicator (Miller 2001).

As Darwin (1871) noted, female animals are often choosier about their mates, and males often display more intensely than females. Accordingly, Miller (1999) identified a significant sexual dimorphism in cultural production (public paintings, books, music albums and plays). Miller explains this dimorphism with a “cultural courtship model”: human cultural production (i.e., art) functions largely as a courtship display, and the persistent sex difference in public cultural production rates reflects an evolved sex difference in courtship strategies (Miller 1999).

Criticism of Miller’s proposal mainly focuses on the last two points: the implied competitiveness for mates that drives art and the claim that the sexual dimorphism[37] of art production that Miller identified in recent western society can be universalized. Critics stress the importance of tradition, which constrains individual competition and promotes cooperation among group members in traditional societies (Dissanayake 2001; Coe 2003). They argue that the bulk of human visual art has been traditional and our perception is biased by an overemphasis on certain short periods where individual creativity and competitiveness were important, such as the Renaissance (Coe 2003). The western non-traditional individualistic society of today is not representative but rather an exception. Moreover, if artists today are driven by competition, it is perhaps for media attention, not for mates. Another problem with Miller’s proposal is that in traditional societies, females are sometimes the main producers of art (Dissanayake 2001; Coe 2003).

Boyd and Richerson’s proposal

If traditions are capable of consistently influencing the human phenotype, meanwhile significantly constraining individual competition in favor of the genes of that individual,[38] it may arguably be necessary

[37] Sexual dimorphism is a measure of differences between the sexes (e.g., height, color, etc.), mostly due to the operation of sexual selection.
[38] Thus reducing the genes’ relative importance in determining human behavior.

to incorporate culture into the Darwinian framework as an inheritance system that is partly independent from the genetic inheritance system. This is what Boyd and Richerson (1985) dubbed "Dual Inheritance Theory". They pointed out that Darwin's theory does not explicitly distinguish cultural inheritance from genetic inheritance. Darwin was a self-declared Lamarckian who believed that acquired variation (through social learning, e.g., a mechanism that transmits cultural information) played an important role in evolution (Richerson and Boyd 2001). So, Darwin's assumptions about beauty and evolution, which we mentioned in the introduction, should be viewed within a gene-culture coevolutionary framework.

Thus, within this framework, Darwinian selectionism is not exclusively applied to the genetic level but to both the genetic and cultural levels. Also, how both inheritance systems interact in human evolution (i.e., gene-culture coevolution) is investigated in a formalized manner (Boyd and Richerson 1985, 2005). Analogous to how population geneticists model the way different forces change gene frequencies in a population, they model how forces interact to bias cultural transmission in a population — that is, how culture[39] evolves. In Dual Inheritance Theory, the evolution and maintenance of culture is described by several mechanisms including transmission bias. One of these mechanisms or forces is "indirect" or "model" bias (Henrich and McElreath 2003; McElreath and Henrich 2007). Boyd and Richerson (1985, ch. 8) postulated that this force might cause a "cultural runaway process" that in turn offers an explanation for the evolution of aesthetic traits and art. In short, individuals imitate successful people because they provide the highest chance of acquiring adaptive information (Flinn and Alexander 1982). They prefer a certain value of an indicator of success (e.g., number of children or acres of land). This system of indicator trait and preference trait can, under certain conditions, be caught in a runaway process. A self-enforcing feedback loop between indicator and preference can cause the indicator trait, which was initially an adaptive sign of success, to become exaggerated following its own internal logic. "Much as peacock tails and bowerbird houses are thought to result from runaway sexual selection, the indirect bias runaway process will generate traits with an exaggerated, interrelated, aesthetically pleasing but afunctional form" (Boyd and Richerson 1985, p. 278).

As we suggested before, the fact that women clearly also engage in art production, especially in traditional societies, which are the rule in human evolution, but also fairly recently in the emancipated west, poses a problem for Miller's argument that art making is a sexual adaptation since it strongest support is the

[39] The term culture refers here not to a specific culture, but to "information" (ideas, beliefs, etc.) which is transmitted in a population through social learning.

apparent sexual dimorphism in art making, with men showing off artistically and women choosing. In his contributing chapter to the book "The evolution of culture", Miller (1999) uses data on human sexual dimorphism in "cultural output" (i.e., art making) as evidence for the operation of sexual selection. Sexual dimorphism is one of the most convincing proofs one can find for sexual selection operating, since sexual selection is the main cause of sexual dimorphism in organisms. As Darwin (1871) noted, since female animals are often choosier about their mates (because they usually invest more in less offspring than males), males may evolve quite elaborate displays as a response to female choosiness. The conspicuous sexual dimorphism in the peafowl is a clear-cut example: peacocks have large and costly tails, peahens are drab in color, differences that are obvious consequences of sexual selection. So Miller states that a work of art is like a peacock's tail: very costly, but compensated by reproductive success and thus adaptive.[40] There are at least two problems with this "empirical support" for Miller's proposal that art making evolved as a male sexual adaptation. Firstly, mating succes is a poor proxy for reproductive succes in post-birth-control cultures (also see Fitch 2006). Secondly, the sample of artists Miller (1999) uses (jazz musicians in the west prior to female emancipation) is not representative for humans in general. In many traditional societies women also engage in elaborate artistic behavior. Miller (2000) may have realized the shortcomings of his sexual dimorphism argument when he subsequently suggested in his book "The mating mind" that art making may be the result of a special kind of sexual selection, namely, *mutual* sexual selection. Under mutual sexual selection both males and females evolve sexual ornaments, consequently dissolving the sexual dimorphism. In the case of art, both men and women would have evolved to make art in order to attract mates and appreciate art to assess mates. However, by abandoning the sexual dimorphism argument, which is a strong one for sexual selection, the case for art as a sexual adaptation is severely weakened. All other aspects of art (its costliness, its captivating capacity, etc.) can easily be explained by other processes. Furthermore, if art evolved under mutual sexual selection it would predict that men are specifically interested in female art and women in male art. However, at first sight, the reverse might be the case, people especially being interested in art from same-sex peers. In fact, this would

[40] The peacock's tail could only have evolved if the survival costs of having one are compensated by its reproductive benefits. In other words, there is an evolutionary tradeoff between investing in survival and in reproduction. Imagine there are 2 types of peacocks in a population. There are 20 type 1 peacocks with less attractive but also less risky tails, half of which reach reproductive age. Type 2 peacocks have enormous, conspicuous tails, and there are also 20 of them in the population. As a result, 19 type 2 peacocks are eaten by tigers and only one of them survives to reproductive age. If, however, this one male is so attractive in comparison to the others of group 1 so that he acquires, say, 90 % of the matings, the trait of the enormously large tail will spread over the population and persist at the expense of smaller tails, regardless of the high fatality it causes among males, because its mean evolutionary payoff is higher.

be highly consistent with SE, since the more the maker and the experiencer of art are similar, the more their pre-existing biases will be (also see 3.3.2.) .

Boyd and Richerson offers another possible way out of this problem as in their cultural model the sex of the individuals do not play a role:

> Notice that in the case of the cultural runaway process colorful displays are not as likely to be limited to the male sex as they are with the genetic analog. A prestigious male or female can have an unlimited number of cultural offspring by non-parental transmission, whereas in the genetic case only males can take advantage of multiple matings to increase their fitness enough to compensate for costly displays. The fact that women as well as men participate in elaborate symbolic behaviors is more consistent with a cultural than with a genetic runaway explanation. (Boyd and Richerson 1985, pp. 278-279)

This cultural hypothesis about art illustrates that application of sexual selection models to the evolution of art doesn't imply that art needs to have a sexual function. The model, in this case Fisher's runaway, is assumed to apply to non-sexual cultural transmission as well. However, we will argue that the concept of SE applied to art implies a runaway process (which is a secondary force resulting from indirect benefits as we have mentioned above) is not even required for aesthetics and art to evolve. Exploitation of sensory biases — a primary force — can do the trick just as well.

The concept of Sensory Exploitation

Our proposition is based on the observation that both existing proposals show how sexual selection theory applied to artistic behavior offers valuable mechanistic insights into its evolution, but that they may underestimate the importance of SE in sexual selection and as such in the evolution of art. We will argue that SE may need to play a more substantial role in the evolutionary approach to art just like it does today in sexual selection theory. Art is believed to lie at the heart of culture, so if any behavior should be considered from a gene-culture coevolutionary perspective it must be artistic behavior. Thus, we will not a priori exclude the influence of cultural transmission from our model.[41]

As stated, we view "artistic behavior" as producing and experiencing signals (or a perceivable object emitting signals) with captivating meaning and/or form (design) to group members. The distinction between aesthetics and meaning made in most contemporary definitions of art roughly corresponds to the distinction made by Arnqvist (2006) between hidden preferences influencing the design of signals and adaptive sensory biases influencing the content of signals, resulting in mimicking signals, respectively. Thus, from a broad signal evolution perspective we can state that what Van Damme (2008, p. 30) has called aesthetics, corresponds to design and results from the exploitation of hidden preferences, and what he has called "meaning" corresponds to content and results from exploitation of adaptive sensory biases by mimicking signals or traits.

Elaborating on the discussion in section 2, let us first consider the origin of artistic behavior. Pre-existing biases of the psychosensory system are the most plausible candidate for many of the origins of female mate preferences, influencing which male display traits will evolve (e.g. Arnqvist 2006). Analogously, human pre-existing psychosensory biases may influence the direction in which art evolves. Our argument is that by focusing upon an indirect-benefit model this influence may be underestimated. For example, Miller (1998, p. 107) argues against the sensory bias evidence that "latent preferences are not necessary, according to R. A. Fisher's (1930) runaway theory. Even chance fluctuations in mate preferences, combined with a strange kind of evolutionary positive-feedback loop, could produce quite extreme mate preferences and quite exaggerated courtship traits." However, this argument can be easily reversed: Why do you need to postulate a combination of chance fluctuations and a secondary process such as Fisher's runaway when "latent preferences" are inevitably present anyway (see Kirkpatrick and Ryan 1991, Arak and Enquist 1995)? As mentioned, this critique also applies to Boyd and Richerson's runaway model. SE delivers a more parsimonious explanation for the origin and evolution of aesthetics — although it does not exclude secondary processes such as runaway. Miller (1998, 2000) also tends to minimize the sensory bias model by limiting it to preferences that are mere side-effects due to engineering details of the sensory system (i.e., *hidden preferences),* ignoring *adaptive sensory biases*. That adaptive sensory biases influence the

---

[41] Notice, however, that Dual Inheritance Theory does not exclude that art could have been sexually selected; e.g., Boyd and Richerson (1985, p 277): "Cultural traits which affect mating preference could similarly affect genetic evolution through the action of sexually selection."

evolution of male traits is evidenced by clear-cut cases of mimics as sexual displays (Fuller et al. 2005). Consider the classic example used to explain Fisher's runaway process, the peacock's tail. Ridley (1981) suggested that tails with multiple eyespots, such as those of the peacock and the Argus pheasant, play upon a widespread responsiveness to eye-like stimuli in animal perception. In certain cases runaway is definitely limited by the need to maintain mimicking function. Miller (2000, p.142ff.) also voices the concern that a sensory bias model ignores the importance of an organisms' avoiding having sexual preferences for any ornaments that offer no fitness benefit or negative fitness benefit to them (surely there would be selection against this?). This concern is again easily addressed with the argument of stabilizing selection mentioned before: selection against adaptive sensory biases is unwarranted since they serve crucial functions in other, non-mating contexts. Another concern of Miller (2000, p. 146) is that: "For highly social animals like most primates, finding potential mates is not the problem. Many primates already live in large groups, and interact regularly with other groups. They are spoiled for choice. When mate choice depends more on comparing mates than locating mates, the sensory engineering argument seems weaker." It may be that in animals living in social groups sensory exploitation is less important than in solitary animals. However, we would like to stress that although the argument is contra sensory exploitation it is not necessary pro good genes selection. In social animals intra-sexual selection becomes more important, resulting in the development of weapons (such as antlers) rather than appealing ornaments (Andersson 1994). Moreover, the assumption that social animals *compare* mates already implies they are looking for good genes. Finally, Miller reduces sensory exploitation again here to engineering details. When males evolve mimics to mislead females, competition between males is guided by the success of the mimic in eliciting a response and not by comparison between mates.

Another important criticism of Miller's proposal is that he does not really grasp what Fisherian runaway and costly signaling means (Haufe 2008). Miller (2000, p. 147) employs the following reasoning against SE, arguing that sensory biases will always be entrained by good genes selection: "[i]f sensory biases led animals to choose lower-fitness animals over higher-fitness animals, I suspect that the biases would be eliminated rather quickly." However, as Haufe (2008, p. 124) explains:

> Genetic modeling of sexual selection does not confirm Miller's suspicions. In fact, it directly contradicts them. ..., it follows analytically from the most basic Fisherian runaway model (as well as from other kinds of models) that a preference which causes (say) females to prefer "lower-fitness" (i.e., lower viability) animals over "higher-fitness" (i.e., higher viability) animals can spread and persist in a population, even when a preference for "optimal" (in terms of viability) males is

> introduced. Not only that, according to the basic model the preference which initiated runaway will itself become exaggerated, causing males to have even lower viability. Miller presumably is aware of this feature of runaway. However all of this gets tossed aside in pursuit of "hidden adaptive logic."

So, the strong version of our concept predicts that SE not only exerts a substantial influence on the direction in which art evolves, but that it may also maintain artistic behavior. In section 2 we explained how this is theoretically possible in the evolution of male display traits. Analogously, this possibility applies to the evolution of art making. It is clear from the evidence in sexual selection that the primary force of SE will always be present. The same applies to art. Secondary forces, such as indirect benefits may be operating but are in principle not required for art to evolve. So here we explore how far we can get without a priori invoking these secondary processes.

Iconic representation

The role of perceptual biases in the evolution of art has already been extensively investigated by several researchers (e.g., Hodgson 2006; Kohn and Mithen 1999; Ramachandran and Hirstein 1999). Essentially, they all have focused on the abstract, geometric aspect of visual art. They state that art emerged because its geometric patterns are supernormal stimuli to the neural areas of the early visual cortex. As such (exaggerated) symmetry, contrast, repetition, and so on, in visual art hyperstimulate these early neural areas. Thus, they have focused on what we have called hidden preferences. We agree with these authors that hidden preferences probably play an important role in the design aspects of human visual representations as they do in the design of male display traits.

However, as indicated by Van Damme's definition, design is only one aspect of human visual art – content, or meaning (mimics/iconic representations as the result of adaptive sensory biases) is at least as important in most cases. We will make this clear by way of an example — a comparison between egg spots in cichlids and visual art in humans from a semiotic viewpoint. This is followed by an introduction to some of the human adaptive sensory biases exploitable by iconic representations.

Semioticists generally agree that biological mimicry is a semiotic phenomenon (Maran 2007). In his essay, "Iconicity," Sebeok (1989) demonstrates that mimicry is a case of iconicity in nature. "A sign is said to be iconic when the modeling process employed in its creation involves some form of simulation" (Sebeok and Danesi 2000), and this is exactly what happens when adaptive sensory biases are exploited. We suggest that this also works the other way around: not only are mimics icons, visual art, or more specifically iconic representations (i.e., realistic art, figurative imagery) can be usefully perceived as mimics resulting from exploitation of human adaptive sensory biases.

Van Damme (2008, p. 38) defines iconic representations as: "The two- or three-dimensional rendering of humans and other animals, or to be more precise, the representation of things resembling those in the external world, or indeed imaginary worlds, fauna and flora especially, but also topographical features, built environments, and other human-made objects." This definition is equally applicable to mimics. We have discussed the case of the egg spots in section 2. What is interesting for the problem of the evolution of human representational art, is that cases of mimicry like this one show how ordinary selection via SE can produce two-dimensional representations (the egg spots) on a surface (the anal fin of the male) of three-dimensional objects (the eggs). To a female cichlid both the signal from the egg and the signal from the egg spot mean "egg", in the sense that she responds indiscriminately towards both those signals with a sucking reaction. In the same way, humans react towards iconic representations — even though we might "know" we are dealing with an illusion — as we react to the real thing. However, there is a difference between humans looking at art and the female cichlid looking at the egg spots: she really is deceived, whereas we know we are looking at a painting of a landscape and not at the real thing. But does this distinction really matter? Not materially. For even though we know that, say, the movie or novel is not real, we still become deeply emotionally involved. Even though we know it is fiction, we react as if it is not. Art exploits our visual system in the case of iconic representations and our emotional and cognitive biases in general, regardless of our consciousness of the distinction between fiction and reality. Human iconic representations are mimics and as such also result from SE. Of course the female reacts toward formal features, design in other words, but this design is not *just* design but design designated to evoke meaning in order to exploit her.

So instead of focusing on geometrical patterns resulting from exploiting activation of early visual areas of the cortex, we focus on the exploitation of perceptual and mental biases for iconic images, that is, on a higher level of visual processing, say, face recognition. Humans have a hair-trigger response to faces. Everywhere we look, we see faces. In cloud formations, in Rorschach inkblots, and so on. The "fusiform face area" is a part of the human visual system, which may be specialized for facial recognition (first described by Sergent et al. 1992). It has recently been suggested that non-face objects may have certain features that weakly trigger the face cells. In the same way objects like rocky outcroppings and cloud formations may set off face radar if they bear enough resemblance to actual faces (Tsao and Livingstone

2008). Whether the hair-trigger response to faces is innate or learned, it represents a critical evolutionary adaptation, one that dwarfs side effects. The information faces convey is so rich — not just regarding another person's identity, but also their mental state, health, and other factors. It's extremely beneficial for the brain to become good at the task of face recognition and not to be very strict in its inclusion criteria. The cost of missing a face is higher than the cost of declaring a non-face to be a face. So, face recognition is an adaptive sensory bias, which is highly susceptible to exploitation by a depiction of a face as a side effect. If our brain had been less sensitive to faces and had stricter inclusion criteria, perhaps many fewer portraits would have been painted throughout art history.

However strong the bias for faces is, it is not always exploited. In fact, in many prehistoric iconic representations, the face is not extensively elaborated. This is probably due to the specific context in which the depiction is produced and experienced (analogously, it might be that female cichlids are much less sensitive to "egg-like signals" a long time before spawning or after spawning). In many representations of the human figure much more attention is given to specific parts of the body. For instance, in the well known upper paleolithic "Venus" figurines, the head is rather schematic whereas breasts, buttocks, and belly are sculpted in great detail and disproportionately exaggerated. Many different hypotheses have been proposed to explain these distorted female representations (for an overview see McDermott 1996). While speculative, McDermott's (1996) interpretation is particularly interesting for our approach. He proposes that these disproportions resulted from egocentric or autogenous (self-generated) visual information obtained from a self-viewing perspective. In other words, the disproportions in Venus figurines result from the position of the female creators' eyes relative to their own bodies. Self-exploitation of perceptual biases[42] may have been the first step in the emergence of iconic art (Verpooten and Nelissen 2010; Chapter 7). Whether these Venus figurines were created as self-representations, as fertility symbols or as erotic items, and whether they were created by men and/or women, they may constitute material evidence of strong adaptive sensory biases for above-mentioned parts of the female body.

Another frequently recurring theme in art history and even more so in art prehistory is the depiction of animals (large wild animals are among the most common themes in cave paintings). Again, a set of adaptive sensory biases might be one of the underlying causes of the tendency to depict animals. In particular, some have speculated that this could well be drawn back to the shared human capacity for

[42] In this case the adaptive attention toward vital, reproductively functional parts of her own body.

"biophilia" (Wilson 1984). Biophilia is defined as a biologically based or innate predisposition to attend to, or affiliate with, natural-like elements or processes (Kellert and Wilson 1993). This set of tendencies is claimed to be the result of human evolution in a natural world in which human survival significantly depended on interactions with natural elements and entities, such as animals (animals could be, for example, predator or prey). Leading biophilia theorists have characterized it as including both positive and negative affective states towards natural-like elements.[43] These affective states may be exploitable by artificial natural-like signals, such as iconic representations of natural elements. For instance, the depictions of large cats in the Grotte Chauvet (believed to be one of the oldest two-dimensional iconic representations) might have elicited a fear response, drawing attention to the depiction. What art needs to be maintained, improved, and reproduced over different generations, in other words to become a "tradition", is to have attention drawn to it by exhibiting captivating or even gripping aesthetics and/or meaning.

Self-exploitation

Visual art is extra-corporal. A consequence of its extra-corporal aspect is that it is equally perceivable by its producers as by its receivers. When producers are also perceivers and possess more or less the same sensory system with comparable psychosensory biases, SE would predict they are equally prone to exploitation as any other receivers. In other words, same species SE via extra-corporal traits implies the possibility of self-exploitation. Such a self-exploitation would be evidence that traits can be exploitative without any direct or indirect benefits. And it exists. Courting male fiddler crabs sometimes build mounds of sand called hoods at the entrances to their burrows. It has been shown that burrows with hoods are more attractive to females and that females visually orient to these structures. Interestingly, a recent study showed that males themselves were also attracted towards their own hoods as a consequence of SE or sensory trap (Ribeiro et al. 2006). Hence, hood building causes self-exploitation. The same may apply to human visual art. As artists are always the first ones to perceive their artworks, they are most likely the first ones to be exploited by the signals they produce. Miller (2000) likes to use Picasso as an example of a successful artist, who produced a lot of paintings and had a lot of mistresses, to support his hypothesis that art evolved as a sexual display of good genes. But maybe Van Gogh, who hardly sold any paintings

[43] Some also make a distinction between biophilia and biophobia: the former refers to positive, while the latter to negative affective states towards natural-like processes and elements (see Ulrich, 1993). This however seems largely a terminological discussion. The crux of the matter is that there are some biologically-based affective responses to biological categories.

during his lifetime nor had a lot of success with women, to say the least, and locked himself in an attic so to speak to devote himself to his art — to self-exploit his psychosensory biases, is more exemplary of artistic behavior?

Art as a spandrel

In Boyd and Richerson's (1985, ch. 8) cultural runaway model aesthetic traits are maintained as non-functional byproducts of the otherwise adaptive indirectly biased cultural transmission. In our SE concept, we entertain the possibility as well that art, resulting from exploitation of sensory biases, is non-functional. At least, we argue art does not *need* to be functional to have evolved in humans. At certain times and places throughout human evolution, producing and experiencing iconic representations may have been neutral or even maladaptive, depending on specific conditions. The question as to whether visual art such as iconic representations is or has been adaptive or not is thus a tricky one, and hard to answer. Illustrative of this are the divided opinions on adaptiveness of visual art (e.g., Pinker 2002). Moreover, under the proponents of art as adaptive there is no consensus in what way it actually is. To some it is a sexual adaptation (e.g., Miller 1998, 1999, 2000, 2001), to others it is a group bonding adaptation (Coe 2003; Dissanayake 1992, 2001). We conclude that if it can be shown that iconic representations evolve even when they are maladaptive, they definitely will do so when they induce some kind of benefits on any kind of unit of selection. It is a well-known fact in evolutionary biology that the evolutionary function(s) of a particular trait often change substantially over time (cf. Reeve and Sherman, 1993). As stressed by Williams (1966) in his foundational work, adaptation is an "onerous concept" to be demonstrated, not assumed. So, instead of a priori assuming adaptiveness, parsimony demands that we first explore whether art could have evolved even without any adaptive function at all. On our view art can evolve without any adaptiveness assumptions, as a mere consequence of SE. As stated, to the experiencer of a work of art there might be no direct utility involved, just as the female that is mislead by the male mimicking food may not benefit from being sensorily fooled. Here we are not interested in the reproductive success of the artists, but in the (reproductive) success of artistic signals themselves, that spread through cultural transmission[44] regardless of beneficial effects to individuals that transmit them, just as male ornaments

---

[44] There are some indications from the archaeological record that iconic art production is a mainly culturally transmitted behavior, while the ability to experience and interpret art is not and does in fact predate art production, just as the origin of female sensory biases leading to mate preferences sometimes predates exploitation (e.g., Ryan 1998). One of these indications is provided by Hodgson (2006). He remarks that the "first art", both (pre)historical and developmental (children's first drawings are abstract patterns), is geometric. So what he calls "geometric

evolve through sensory exploitation without the need of any benefits to the females. In this sense, it follows from the SE perspective that iconic art making could have evolved as a culturally transmitted spandrel. Spandrels are byproducts of adaptive capacities but not specifically adaptive themselves, borrowing an architectural term for a necessary but non-functional concomitant of primary load-bearing functions (Gould and Lewontin 1979). In this view, art evolved as a byproduct of sensory biases on the part of experiencing art. (On the part of art making it may have evolved as a byproduct of adaptive skills in tool use, among other things.) If this artistic behavior does not impose too much costs upon its practicioners in an initial phase, art may have emerged spontaneously, exploiting their biases, without any utility. It may, however, subsequently be exapted by delivering benefits to art producers and/or experiencers.

A comparison with religion

Recently there has been a surge of interest in the biology and evolution of religion (e.g., Atran 2002; Culotta 2009; Dawkins 2006, ch. 5; Wilson 2002). Research results in this more intensely studied area may be useful to the study of art. From an evolutionary perspective, religion and art seem to have a lot in common. For one thing, both are complex human behaviors that cannot be explained easily in evolutionary terms. An adaptive explanation based on one selective pressure does not suffice for neither. Religion has maladaptive aspects, probably some functional aspects as well; however, just as in the case of art, depending upon specific conditions and as such varying across populations and cultures in human evolution (for examples, see Atran 2002).

Another interesting similarity between art and religion is that they are both based on some form of primary non-functional deception or illusion (and, as said, possible beneficial "after"- effects only crop up on a secondary level). We have typified art as such from the SE perspective, and in evolutionary religious studies too it is stressed that "[a]ll known human societies, past and present, bear the very substantial costs of religion's material, emotional, and cognitive commitments to factually impossible worlds" (Atran 2002, p. 4). This has two, closely linked, interesting consequences for our discussion. Firstly, the SE perspective may be a useful conceptual tool for evolutionary religious studies too; perhaps some form of SE plays a role in

primitives" predates iconic art. Hodgson further notices that no culture has ever been shown to have an iconic art tradition without a geometric tradition, but vice versa, some cultures only have a geometric tradition. He draws from this that the making of geometrics may be a more accessible process than the making of representational motifs and that knowledge of geometrics may be innate whereas, we could add, making representations is not and requires individual learning and social transmission of skills to be evolutionary maintained.

the creation of religious deceptions as it does in art. Secondly, maybe some perceptual or mental biases known to play a role in the creation of religious deception play a role in artistic creation as well. In fact, there is at least one possible candidate for this, similar to the tendency to see faces where there aren't any as a result of a strong bias for face recognition, mentioned above. It is the trip-wired tendency to attribute random events or natural phenomena to the agency of another being, which has been described as a "hypertrophy of social cognition." According to the emerging cognitive model of religion, we are so keenly attuned to the designs and desires of other people that we are hypersensitive to signs of "agents": thinking minds like our own.[45] These findings suggest we all have a bias from childhood to see the natural world as purposefully designed. It's a small step to suppose that the design has a designer. This predisposition to "creationist" explanations has resonance with another tendency in the human mind, the "hypersensitive agency detection device": looking for a thinking "being" even in nonliving things. In classic experiments in the 1940s, psychologists found that people watching animations of circles, triangles, and squares darting about could identify various shapes as characters and infer a narrative (this passage about agents and religion is taken from Culotta 2009). So, exploiting the strong tendency to attribute agency to nonliving things, may have played an important role in the evolution of art as well (and in addition, the experiments also showed evidence of our tendency to make *narratives* with these agents, likely this is also an important tendency exploited in many different arts). In fact, biophilia, which we discussed earlier as a human bias exploited by depicted animals in cave art, might result from a combination of an hypersensitive agency detection device and the capacity to feel empathy for agents. This possibility should be further explored. Maybe it explains the intense emotions of connectedness with "something larger" that "tree huggers" report to experience.

On this note, this might explain people's disinterest for (post)modern art (especially "concept art"): this kind of art is not developed to captivate our attention through exploiting our agency detection device nor our empathic faculty, rather it is designed to investigate and analyze these responses to art (or to "deconstruct" them as contemporary art theorists would say). It is as if artists switched from the animistic method to the scientific method. Indeed as follows from the studies cited in Culotta (2009, p.785) "scientific literacy" requires "an uphill battle", so too seems to be the case with most modern art.

[45] For instance, in an experiment in which undergraduates had to respond under time pressure, they were likely to agree with nonscientific statements such as "The sun radiates heat because warmth nurtures life" (Culotta 2009).

Conclusion

Darwin's theory of sexual selection provides a mechanistic basis to explain the evolution of male sexual display traits. This mechanistic approach has proven useful to developing hypotheses about the evolution of human art. Both Boyd and Richerson (1985, ch. 8) and Miller (1998, 1999, 2000, 2001) have applied an indirect-benefit model to the evolution of artistic behavior. We have argued that the mechanistic possibilities SE has to offer have remained underexplored so far, so we have proposed a concept based upon it and we have used it to evaluate these hypotheses.

Central to SE, being closely related to biological mimicry, is that it is in principle a non-functional or even counterfunctional (maladaptive) evolutionary process with regard to the receiver of signals, merely being driven by exploitation of the receiver's sensory biases. Applied to the evolution of human art, we considered these signals as being culturally transmitted spandrels, non-functional evolutionary byproducts of other traits, namely human perceptual and mental biases such as face recognition and agency detection device. This non-functional view on art has some interesting consequences.

Firstly, in both Miller's and Boyd and Richerson's model, "aesthetic preferences" and "aesthetic traits" (i.e., art) coevolved as a result of an indirect-benefit process that may derail into the Fisherian Runaway Process. We have shown, however, that it follows from the SE perspective that at least some of these aesthetic preferences already should exist *before* any aesthetic traits have evolved. The fact that the aesthetic preferences that are exploited in art are also elicited by non-art, like a natural phenomenon such as a tree, may be an indication of this. Moreover, art is not just about pleasing aesthetics. Meaning — pleasing or not — is also important in art. Analogously, meaning is important in SE of which the exploiting traits are mimics, such as egg spots that represent eggs. So, SE also covers the important characteristic of art that it represents something outside the art context.

Secondly, on this non-functional view it follows that art emerged spontaneously in human evolution by exploiting pre-existing biases and not because it was selected for. As we have hoped to show, benefits are not prerequisite for art to evolve. It would be strange if they were, since on the one hand art today imposes costs without convincing evidence of compensation on any level (cf. Fitch 2006 for music) and since one would expect adaptiveness to differ considerably in populations across time and place (cf. Reeve and Sherman 1993), while nevertheless art is and has been universal for a long time. So, if the costs art usually imposes are not detrimental to the survival of individuals of a population engaging in artistic behavior, it may be borne by the carrying capacity[46] of this population. In fact it follows from our model that it is this carrying capacity of the population that limits the proliferation of culturally transmitted spandrels. If carrying capacity is high we expect high cost art and a lot of it, if it is low we expect the opposite, at equilibrium. As said, all cultures exhibit lower cost abstract art but not all cultures exhibit representational art, which imposes higher costs, for example in terms of time and energy invested in learning and passing on skills (Hodgson 2006, Verpooten and Nelissen 2010 (Chapter 7)). It would be interesting to see whether there is a correlation between the occurrence of representational art and carrying capacity across populations. Hollywood, video games, and virtual reality are the cave art of today and in absolute terms they are obviously much more costly than cave art; maybe they are the direct result of the exceptionally high joint carrying capacity of current industrialized populations in combination with being culturally transmitted spandrels emerging naturally from exploiting our biases.

Thirdly, compensating for the costs or not, beneficial effects might influence the evolution of art on a secondary level. There are at least two types of possible benefits which may exert selective pressures on the evolution of art. One is transmission of valuable (functional) information through art. Some art may have evolved adaptively as a means of storing and transmitting valuable information. This is an appealing proposition; however, its role may not be so important. Why use art if you have language, which may plausibly be a far more efficient instrument to transmit and maintain information? Art may, however, instead of transmitting information itself be useful in *facilitating* transmission of information through language (such as the use of rhyme for better memorizing). Anyway, this possibility should be somehow taken into account in the above-suggested test, because it would mean some sort of compensation for art's costs. The second possible benefit was discussed in great detail in this chapter: the individual (male) benefit of increased reproductive success. When exactly this kind of secondary process will operate, should be further explored. Fuller et al. (2005) have suggested a number of tests to distinguish SE from other preference models in sexual selection in practice. These tests may be used for the same purpose regarding the relative role of SE and indirect-benefit processes in the evolution of artistic behavior.

[46] According to Boyd and Richerson (1985, p. 278) each culture may contain a number of non-functional or counterfunctional traits at equilibrium. By carrying capacity we mean the number of non-functional or counterfunctional cultural traits a population of social learners can maintain. We suggest it depends on the utility of other traits in the population that compensate for the costs of counterfunctional traits, such as technological skills and on the size of the population (a larger population can sustain more costly traits), among other things (cf. Shennan 2001; Henrich 2004).

However, even if indirect benefits prove to play some role under certain conditions, it would not disconfirm the SE view on the evolution of art. If art were a sexual adaptation, it would not lower the costs for the population as a whole. So it does not undermine our prediction of a relation between carrying capacity and abundance of costly art in a population.

Even if art proves to have been adaptive most of the time in human evolution, to individuals as a mating display, to groups as a container of valuable information or as a facilitator of bonding, it will draw upon existing perceptual and mental biases. As a consequence, all of the major hypotheses about art will need to make use of the SE concept, which will need to play a central role in articulating all of them.

Acknowledgements

We thank two anonymous referees, the editors of this volume, Johan Braeckman, Andreas de Block, Tijs Goldschmidt, Yannick Joye, and David Sloan Wilson for sharing useful suggestions and/or commenting on earlier drafts. Also many thanks to Lokaal01_Antwerpen (www.lokaal01.org) for the opportunity to discuss our ideas among scientists and artists. We thank the Konrad Lorenz Institute for Cognition and Evolution Research for the support. Last but not least we thank Thomas Reydon and Katie Plaisance for having us at the conference.

References

Adajian, T. (2007): "The Definition of Art", in: E. N. Zalta (Ed.), *The Stanford Encyclopedia of Philosophy (Fall 2008 Edition)*, http://plato.stanford.edu/archives/fall2008/entries/art-definition/

Andersson, M. (1994). *Sexual Selection*. Princeton: Princeton University Press.

Arak, A. and Enquist, M. (1993). Hidden preferences and the evolution of signals. *Philosophical Transactions of the Royal Society of London,* Series B (340): 207-213.

Arak, A. and Enquist, M. (1995). Conflict, receiver bias and the evolution of signal form. *Philosophical Transactions of the Royal Society of London,* Series B (349): 337-344.

Arnqvist, G. (2006). Sensory exploitation and sexual conflict. *Philosophical Transactions of the Royal Society of London,* Series B (361): 375-386.

Atran, S. (2002). *In Gods we Trust: The Evolutionary Landscape of Religion*. New York: Oxford University Press.

Autumn, K., Ryan, M. J. and Wake, D. B. (2002). Integrating historical and mechanistic biology enhances the study of adaptation. *Quarterly Review of Biology* 77: 383-408.

Basolo, A. L. (1990). Female preference predates the evolution of the sword in swordfish. *Science* 250: 808-810.

Borgia, G. (1995). Complex male display and female choice in the spotted bowerbird: Specialized functions for different bower decorations. *Animal Behavior* 49: 1291-1301.

Boyd, R. and Richerson, P. J. (1985). *Culture and the Evolutionary Process*. Chicago: University of Chicago Press.

Boyd, R. and Richerson, P. J. (2005). *The Origin and Evolution of Cultures*. Chicago: University of Chicago Press.

Burley, N. (1988). Wild zebra finches have band-color preferences. *Animal Behavior* 36: 1235-1237.

Christy, J. H. (1995). Mimicry, mate choice, and the sensory trap hypothesis. *American Naturalist* 146: 171-181.

Coe, K. (2003). *The Ancestress Hypothesis: Visual Art as Adaptation*. New Brunswick: Rutgers University Press.

Culotta, E. (2009). On the origin of religion. *Science* 326 (5954): 784-787.

Darwin, C. (1871). *The Descent of Man, and Selection in Relation to Sex*. 2 vols. London: John Murray. (Reprinted in 1952 by Encyclopedia Brittanica)

Dawkins, M. S. and Guilford, T. (1996). Sensory bias and the adaptiveness of female choice. *American Naturalist* 148: 937-942.

Dawkins, R. (1982). *The Extended Phenotype: The Gene as the Unit of Selection*. Oxford: W. H. Freeman.

Dawkins, R. (2006). *The God Delusion.* Boston: Houghton Mifflin.

Dissanayake, E. (1992). *Homo Aestheticus: Where Art Comes From and Why*. Seattle: University of Washington Press.

Dissanayake, E. (2001). Birth of the arts. *Natural History* 109 (10): 84-91.

Driscoll, C. (2006). The bowerbirds and the bees: Miller on art, altruism, and sexual selection. *Philosophical Psychology* 19 (4): 507-526.

Eibl-Eibesfeldt, I. (1989a). *Human Ethology*. Translated by Pauline Wiessner-Larsen and Annette Heunemann. New York: Aldine Degruyter.

Eibl-Eibesfeldt, I. (1989b.) The biological foundations of aesthetics. In I. Rentschler, B. Hertzberger and D. Epstein (Eds.) *Beauty and the brain: Biological Aspects of Aesthetics* (pp. 29-68). Basel: Birkhauser.

Endler, J. A. (1992). Signals, signal conditions, and the direction of evolution. *American Naturalist* 139: 125-153.

Endler, J. A. and Basolo, A. L. (1998). Sensory ecology, receiver biases and sexual selection. *Trends in Ecology and Evolution* 13: 415-420.

Enquist, M. and Arak, A. (1993). Selection of exaggerated male traits by female aesthetic senses. *Nature* 361: 446-448.

Enquist, M. and Arak, A. (1994). Symmetry, beauty and evolution. *Nature* 372: 169-172.

Eshel, I., Volovik, I. and Sansone, E. (2000). On Fisher-Zahavi's handicapped sexy son. *Evolutionary Ecology Research* 2: 509–523.

Fisher, R. A. (1930). *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.

Fitch, W. T. (2006). The biology and evolution of music: a comparative perspective. *Cognition* 100 (1): 173-215.

Flinn, M. V., and Alexander, R. D. (1982). Culture theory: The developing synthesis from biology. *Human Ecology* 10: 383-400.

Fuller R. C., Houle D., and Travis J. (2005). Sensory Bias as an Explanation for the Evolution of Mate Preferences. *American Naturalist* 166: 437-446.

Gaut, B. (2005). The Cluster Account of Art Defended. *British Journal of Aesthetics* 45(3): 273-288.

Ghirlanda, S. and Enquist, M. A. (2003). A century of generalization. *Animal Behaviour* 66: 15-36.

Gould, S. J. (1991). Exaptation: A crucial tool for evolutionary psychology. *Journal of Social Issues* 47: 43-65.

Gould, S. J., and Lewontin, R. C. (1979). The spandrels of San Marco and the panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society* B 205: 581-598.

Guilford, T., and Dawkins, M.S. (1991). Receiver psychology and the evolution of animal signals. *Animal Behaviour* 42: 1-14.

Haufe, C. (2008). Sexual selection and mate choice in evolutionary psychology. *Biology and Philosophy* 23: 115-128.

Henrich, J. and McElreath, R. (2003). The evolution of cultural evolution. *Evolutionary Anthropology* 12: 123-135.

Henrich, J. (2004). Demography and Cultural Evolution: How Adaptive Cultural Processes can Produce Maladaptive Losses: The Tasmanian Case. *American Antiquity* 69 (2): 197-214.

Hodgson, D. (2006). Understanding the origins of Paleoart: The neurovisual resonance theory and brain functioning. *PaleoAnthropology* 2006: 54–67.

Jersakova, J., Johnson, S. D., and Kindlmann, P. (2006). Mechanisms and evolution of deceptive pollination in orchids. *Biological Reviews of the Cambridge Philosophical Society* 81: 219-235.

Johnstone, R. A. (1994). Female preference for symmetrical males as a byproduct of selection for mate recognition. *Nature* 372: 172-175.

Kellert, S. R. and Wilson, E. O. (1993). *The Biophilia Hypothesis*. Washington: Island Press.

Kirkpatrick, M. and Ryan, M. J. (1991). The evolution of mating preferences and the paradox of the lek. *Nature* 350: 33-38.

Kohn, M. and Mithen S. (1999). Handaxes: Products of sexual selection? *Antiquity* 73 (279): 518-26.

Kokko, H., Brooks, R., Jennions, M. D. and Morley, J. (2003). The evolution of mate choice and mating biases. *Proceedings of the Royal Society* B 270: 653-664.

Lande, R. (1981). Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences of the United States of America* 78: 3721-3725.

Low, B. S. (1979). Sexual selection and human ornamentation. In N. A. Chagnon and W. Irons (Eds.) *Evolutionary biology and human social behavior* (pp. 462-487). Boston: Duxbury Press.

Maran, T. (2007). Semiotic interpretations of biological mimicry. *Semiotica* 167–1/4: 223-248.

McElreath, R. and Henrich, J. (2007). Dual inheritance theory: the evolution of human cultural capacities and cultural evolution. In R. Dunbar and L. Barrett (Eds.) *Oxford Handbook of Evolutionary Psychology*. Oxford: Oxford University Press.

McDermott, L. (1996). Self-representation in upper paleolithic female figurines. *Current Anthropology* 37: 227-275

Miller, G. F. (1998). How mate choice shaped human nature: A review of sexual selection and human evolution. In C. Crawford and D. Krebs (Eds.) *Handbook of evolutionary psychology: Ideas, issues, and applications* (pp. 87-129). Mahwah: Lawrence Erlbaum.

Miller, G. F. (1999). Sexual selection for cultural displays. In R. Dunbar, C. Knight, and C. Power (Eds.) *The evolution of culture* (pp. 71-91). Edinburgh University Press,.

Miller, G. F. (2000). *The Mating Mind*. London: Heinemann.

Miller, G. F. (2001). Aesthetic fitness: How sexual selection shaped artistic virtuosity as a fitness indicator and aesthetic preferences as mate choice criteria. *Bulletin of Psychology and the Arts* 2: 20-25.

Pasteur, G. (1982). A classificatory review of mimicry systems. *Annual Review of Ecology, Evolution, and Systematics* 13: 169-199.

Payne, R. J. H. and Pagel, M. (2000). Inferring the origins of state-dependent courtship traits. *American Naturalist* 157: 42-50.

Pinker, S. (1997). *How the mind works*. New York: Norton.

Pinker, S. (2002). *The blank slate. The modern denial of human nature*. New York: Viking.

Ramachandran, V. S., and Hirstein, W. (1999). The science of art: A neurological theory of aesthetic experience. *Journal of Consciousness Studies* 6: 15–51.

Reeve, H. K. and Sherman, P. (1993). Adaptation and the goals of evolutionary research. *Quarterly Review of Biology* 68: 1-32.

Ribeiro, P. D., Christy J. H., Rissanen R. J. and Kim T. W. (2006). Males are attracted by their own courtship signals. *Behavioral Ecology and Sociobiology* 61: 81-89.

Richerson, P. J. and Boyd, R. (2001). Built for Speed, Not for Comfort: Darwinian Theory and Human Culture. *History and Philosophy of the Life Sciences* 23: 425-465.

Ridley, M. (1981). How the peacock got his tail. *New Scientist* 91: 398-401.

Rodd, F. H., Hughes, K. A., Grether, G. F. and Baril, C. T. (2002). A possible non-sexual origin of a mate preference: are male guppies mimicking fruit? *Proceedings of the Royal Society* B 269: 475-481.

Rodriguez, R. L. and Snedden, W. (2004). On the functional design of mate preferences and receiver biases. *Animal Behaviour* 68: 427-432.

Ryan, M. J. (1990). Sexual selection, sensory systems and sensory exploitation. *Oxford Surveys in Evolutionary Biology* 7: 157-195.

Ryan, M. J. (1995). Female responses to ancestral advertisement calls in tungara frogs. *Science* 269: 390-392.

Ryan, M. J. (1998, review 1999). Sexual Selection, Receiver Biases, and the Evolution of Sex Differences. *Science* 281: 1999-2003.

Ryan, M. J. and Keddy-Hector, A. (1992). Directional patterns of female mate choice and the role of sensory biases. *American Naturalist* Supplement 139: 4-35.

Ryan, M. J. and Rand, A. S. (1990). The sensory basis of sexual selection for complex calls in the tungara frog, *Physalaemus pustulosus* (sexual selection for sensory exploitation). *Evolution* 44: 305-314.

Ryan, M. J. and Rand, A. S. (1993). Sexual selection and signal evolution: the ghost of biases past. *Philosophical Transactions of the Royal Society of London* B 340: 187-195.

Schiestl, F. P. and Cozzolino, S. (2008). Evolution of sexual mimicry in the orchid subtribe orchidinae: the role of preadaptations in the attraction of male bees as pollinators. *BMC Evolutionary Biology* 8: 27.

Sebeok, T. A. (1989). Iconicity. In: T. A. Sebeok (Ed.) *The Sign and Its Masters* (pp 107-127). Lanham: University Press of America.

Sebeok, T. A. and Danesi, M. (2000). *The Forms of Meaning: Modeling Systems Theory and Semiotic Analysis*. Berlin: Mouton de Gruyter.

Sergent, J., Ohta, S. and MacDonald, B. (1992). Functional neuroanatomy of face and object processing. A positron emission tomography study. *Brain* 115: 15-3.

Shaw, K. L. (1995). Phylogenetic tests of the sensory exploitation model of sexual selection. *Trends in Ecology and Evolution* 10: 117-120.

Shennan, S. (2001). Demography and cultural innovation: a model and its implication for the emergence of modern human culture. *Cambridge Archeological Journal* 11: 5-16.

Sober, E. (1984). *The Nature of Selection. Evolutionary Theory in Philosophical Focus*. Cambridge: Massachusetts Institute of Technology Press.

Tobler, M. (2006). Die Eiflecken bei Cichliden: Evolution durch Nutzung der Sinne? (The eggspots of cichlids: Evolution through sensory exploitation?). *Zeitschrift für Fischkunde* 8: 39-46.

Tsao, D.Y. and Livingstone, M. S. (2008). Mechanisms of face perception. *Annual Review of Neurosciences* 31: 411-437.

Ulrich, R. S. (1993). Biophilia, biophobia, and natural landscapes. In: R. S. Kellert, E. O. Wilson (Eds.) *The Biophilia Hypothesis* (pp. 73-137). Washington: Island Press.

Van Damme, W. (2008). Introducing world art studies. In: W. Van Damme and K. Zijlmans (Eds.) *World Art Studies: Exploring Concepts and Approaches*. Amsterdam: Valiz.

Verpooten, J. and Nelissen, M. (2010). Sensory exploitation and cultural transmission: the late emergence of iconic representations in human evolution. *Theory in Biosciences*.

West-Eberhard, M. J. (1992). Adaptation: current usages. In: E. F. Keller and E. A. Lloyd (Eds.) *Keywords in Evolutionary Biology* (pp. 13-18). Cambridge: Harvard University Press.

West-Eberhard, M. J. (1984). Sexual selection, competitive communication, and species-specific signals in insects. In: T. Lewis (Ed.) *Insect Communication* (pp. 283-324). London: Academic Press.

Wickler, W. (1962). “Egg-dummies” as natural releasers in mouth-breeding cichlids. *Nature* 194: 1092-1093.

Williams, G. C. (1966). *Adaptation and Natural Selection*. Princeton: Princeton University Press.

Wilson, E. O. (1984). *Biophilia*. Cambridge: Harvard University Press.

Wilson, D. S. (2002). *Darwin’s Cathedral: Evolution, Religion, and the Nature of Society*. Chicago: University of Chicago Press.

Zahavi, A. (1975). Mate selection: A selection for a handicap. *Journal of Theoretical Biology* 53: 205-214.

Zahavi, A. (1991). On the definition of sexual selection, Fisher's model, and the evolution of waste and of signals in general. *Animal Behaviour* 42(3): 501-503.

Zahavi, A. and Zahavi, A. (1997). *The Handicap Principle: A Missing Piece of Darwin's Puzzle*. Oxford: Oxford University Press.