EVOLUTIONARY INTERACTIONS BETWEEN HUMAN BIOLOGY AND ARCHITECTURE: INSIGHTS FROM SIGNALING THEORY AND A CROSS-SPECIES COMPARATIVE APPROACH

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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.[71]

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[71] 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

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 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. Post-moulds, 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 ecological 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 architectural 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 furlessness 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 perishable, 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, mammoths, 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.

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

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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[72] – 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 occurs 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

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

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*).

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.

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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)

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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 (2012), 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 suitable 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,[73] or biases that are under strong selective pressure in another context than the SE system such as perceptual biases adapted for finding 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 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 findings have been made. Madden

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[73] 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.

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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

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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. 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,[74] which was originally proposed by Orians 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 park-like 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).

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

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 non-animate 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 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 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 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 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 reflects 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: finding 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 significance 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 artificial elicitors. This may lead to a lasting incorporation of these artificial 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 'fight or flight.' 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. Specifically, 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

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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 2012), 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., pilo-erection) (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-

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fication. 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 edifice, 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 edifices 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) insignificance in them, with the result that people are inclined to 'flock 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.

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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). 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 have deployed a biological and evolutionary perspective to human architectural accomplishments. We have distinguished and investigated two main purposes of architecture: a protective function, and a signaling function. Based on a phylogenetic approach, we have 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 have 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.

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