

Chapter 9

Sensory Exploitation: Underestimated in the Evolution of Art As Once in Sexual Selection Theory?

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9.1 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),

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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.¹

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, b). 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

¹ 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).

(such as ornament, song, and dance)² have evolved by appealing to 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 section 2 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,³ cultural runaway process that leads to the spread of cultural aesthetic traits. These two hypotheses are reviewed and discussed in the first part of section 3.

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 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

²Often 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. Here we focus on the former.

³Cultural 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.

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.

9.2 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).

9.2.1 *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 disequilibrium⁴ 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).

9.2.2 *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 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

⁴In 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.

generations these orange spots may become ever more accurate mimics⁵ 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 exaptive⁶ 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 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.

⁵The 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.

⁶An exaptation is a pre-existing trait that acquires a new beneficial effect without modification to the phenotype by selection (Gould, 1991).

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.

9.2.3 *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 selection⁷ 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

⁷Stabilizing 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.

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.

9.2.4 *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 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).

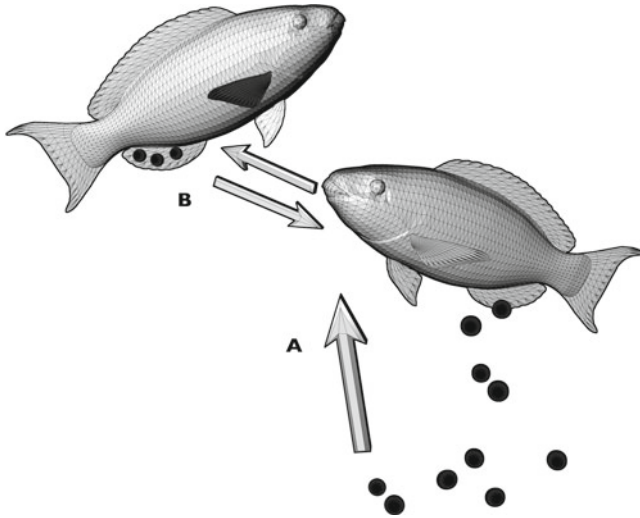


Fig. 9.1 The mating system of mouthbreeding cichlids. (A) After laying her eggs the female (right) sucks them up in her mouth. Her ability to detect the eggs is strongly selected for, since every missed egg results in a reduction of fitness. This ability depends on a hair trigger response to “egg signals.” (B) Subsequently, males (left) evolved egg spots, accurate two-dimensional mimics of 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 real eggs, and there is no reason 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 Verpoeten.)

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) (Fig. 1). 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.

9.2.5 *Summary of section 9.2*

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.

9.3 **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).

9.3.1 *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 dimorphism⁸ 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).

9.3.2 *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

⁸Sexual dimorphism is a measure of differences between the sexes (e.g., height, color, etc.), mostly due to the operation of sexual selection.

individual,⁹ it may arguably be necessary 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 culture¹⁰ 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 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

⁹Thus reducing the genes’ relative importance in determining human behavior.

¹⁰The term culture refers here not to a specific culture, but to “information” (ideas, beliefs, etc.) which is transmitted in a population through social learning.

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.¹¹ 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 success is a poor proxy for reproductive success 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 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

¹¹The 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.

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.

9.3.3 *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.¹²

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

¹²Notice, 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.”

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 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.

9.3.3.1 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.

Semioticians 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 biases¹³ may have been the first step in the emergence of iconic art (Verpooten and Nelissen 2010). 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 “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

¹³In this case the adaptive attention toward vital, reproductively functional parts of her own body.

including both positive and negative affective states towards natural-like elements.¹⁴ 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.

9.3.3.2 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 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?

9.3.3.3 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,

¹⁴Some 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.

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 misled 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 transmission¹⁵ regardless of beneficial effects to individuals that transmit them, just as male ornaments 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

¹⁵There 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 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 (Fig. 2).

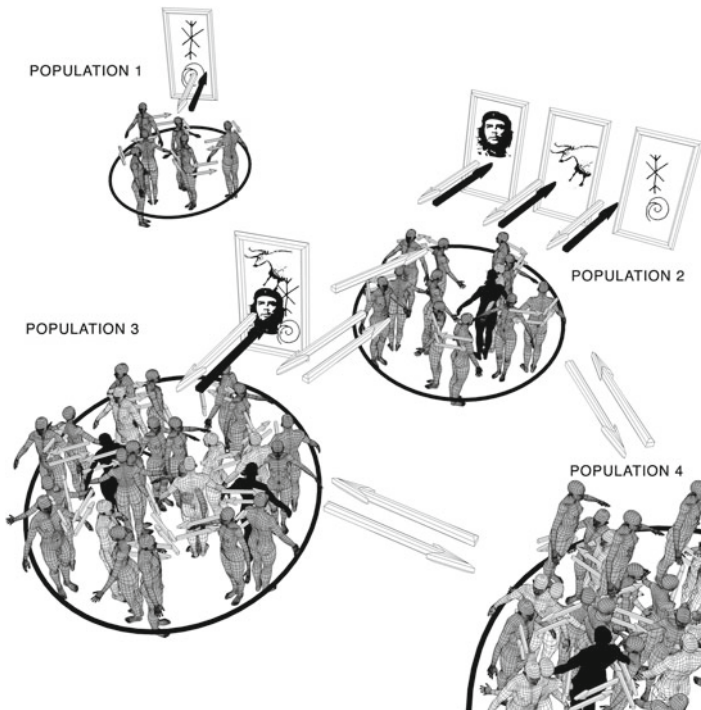


Fig. 9.2 Sensory exploitation, cultural transmission and the influence of the size of the interacting pool of social learners on art. 4 hypothetical populations of social learners and the artworks that they produce are shown. Arrows stand for the direction in which “information” is transmitted. In addition, 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 their own 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 they are large and interconnected, creating an interacting pool of social learners that is large enough for innovations required for production of iconic art to spontaneously accumulate and persist regardless any beneficial effects of the resulting artworks. (artwork: Alexandra Crouwers and Jan Verpooten.)

tool use, among other things.) If this artistic behavior does not impose too much costs upon its practitioners in an initial phase, art may have emerged spontaneously, exploiting their biases, without any utility (Fig. 2). It may, however, subsequently be exapted by delivering benefits to art producers and/or experiencers. For a detailed discussion of the relation between SE, cultural transmission and the emergence of visual artistic traditions, see Verpooten and Nelissen (2010).

9.3.3.4 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 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.¹⁶ 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).

¹⁶For 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).

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.

9.4 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 capacity¹⁷ 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). 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

¹⁷According 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).

same purpose regarding the relative role of SE and indirect-benefit processes in the evolution of artistic behavior. 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.

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