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Signaling and the Cultural Evolution of Art

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Abstract

Why and how does art evolve? Evolutionary psychology has commonly focused on unravelling evolutionary functions of art and experimentally establishing innate cognitive predispositions that might be exploited in art (e.g. attentional preference for animal cues). Cultural evolution research enriches and complements this work. First, studies based on cultural attraction theory establish how such predispositions foster historical convergences in the forms art takes, for instance in renaissance portraiture. Moreover, in line with dual inheritance theory, several lines of evidence indicate a key role for social learning dynamics as well, such as prestige bias driven divergences from innate cognition in contemporary art appreciation. This article points out that, despite their differences, these evolutionary approaches to art have in common that they are grounded in signaling theory. Within this encompassing signaling framework, various art traditions (e.g. the Acheulean hand axe), factors (e.g. ecology and demography), and methods (e.g. phylogenetic comparison) are considered.

Keywords: art, cultural evolution, dual inheritance, cultural attraction, evolutionary psychology, signaling, social learning, prestige bias, innate cognition, art appreciation

Darwin already devoted considerable attention to art and aesthetics in his second major work on evolution (Darwin, 1871). He came to the conclusion that a sense of beauty was the main evolutionary driver of the cultural and biotic aesthetic diversity found in human and non-human animals alike (e.g. ornaments, songs, dances). In recent decades this topic has regained traction, especially in evolutionary psychology, where evolutionary aesthetics has flourished as a devoted sub-branch (Volland & Grammer, 2003). Evolutionary psychology has commonly focused on elucidating evolutionary functions of art as well as experimentally establishing ancestral psychological adaptations that might be exploited in art (e.g. attentional preference for animal cues). However, a common criticism has been that, due to its general focus on Stone Age brains, evolutionary psychology has painted a limited picture of the evolution of human behavior (Laland & Brown, 2006), and art and aesthetics more specifically (Bartalesi & Portera, 2015). Furthermore, evolutionary psychology tends to consider culture as evoked, which means that it regards behavioral differences commonly called cultural to be due to environmental differences to which a shared ancestral human nature adaptively and flexibly responds (Tooby & Cosmides, 1992). This is in contrast to dual inheritance theory, where culture is regarded as a second system of inheritance, next to genes, that has played its own crucial role in shaping human evolution (Henrich, 2017; Richerson & Boyd, 2005). This theory of cultural evolution has been explicitly advanced as an alternative to classic socio-biology and evolutionary psychology.

This article takes a slightly different approach to the matter. Despite obvious differences, it attempts to establish and make use of the complementarity of these evolutionary approaches when it comes to art. For this purpose, first a working definition of art is presented. Then, the two main cultural evolution programs, dual inheritance and cultural attraction, are presented and it is examined how they relate to evolutionary psychology. It is shown that, when it comes to art, these programs have a common ground in signaling theory, the main evolutionary theory about animal communication. Consequently, within this broader signaling framework, diverse and ongoing research is considered that bears relevance on the cultural evolution of art. It is demonstrated how each of the research programs contributes to explaining particular facets of art, from the Acheulean hand axe and Upper Paleolithic figurative art, to renaissance portraiture and contemporary art. In particular, prestige driven expertise-dependent divergences from innate cognitive predispositions in modern art appreciation is brought forward as a revealing example of complementarity of these programs.

Definition

This article uses the term art in accordance with its common dual usage (e.g. Google's English dictionary, Oxford Languages, OUP) to primarily refer to visual art but also, when it is relevant, by extension to other arts such as music (Youngblood, Ozaki & Savage, this volume) and storytelling (Sobchuk, this volume). Despite intuitive agreements on what counts as art, there is little consensus among scholars on how to precisely define it. Therefore, the following working definition is presented attuned to the purposes of this article: art is a cultural, creative, and aesthetic signal that a signaler (e.g. an artist) sends to manipulate a reactor (audience) to the signaler's and possibly, but not necessarily, to the reactor's benefit.

Let us break down this definition. First, it is generally accepted that art is a form of communication. Consequently, signaling theory, which is a coherent theory about the evolution of communication (Dawkins & Krebs, 1978; Maynard Smith & Harper, 2003), allows us to consider art as a signal. In effect, the large bulk of evolutionary approaches regards art as such. A central assumption of signaling theory is that the effect of the signal on the reactor should be beneficial for the signaler, otherwise it would

not have evolved. Second, of particular relevance in the context of this article, art is often considered to have a significant cultural component (Prum, 2013), as indicated for example by larger between than within cultural variability (Fitch, 2015). Third, art is commonly assumed to involve some form of behavioral flexibility and imagination-based creativity (Davies, 2012). This excludes, for instance, cultural innovation through mere accumulation of copying errors. And finally, while the traditionally assumed central role for aesthetics in art has been rightfully disputed (e.g. Brown and Dissanayake, 2009), it arguably remains a necessary characteristic of art. Aesthetic design is taken to be typically moving or striking and to be characterized by complex spatial and often temporal patterns and colors, or acoustic volume, texture, duration, pitch, and hypnotic repetition/rhythm. Aesthetic design may be attractive, repulsive, arousing, seductive, hypnotic, etc. to reactors (De Tiège et al., 2021). There have been intriguing attempts to eradicate the aesthetic from the arts, but history has shown that they have generally been rather unsuccessful. Importantly, aesthetic design does not need to be intended by the artist. To take one—telling—example, it has been argued that even the most influential piece of cerebral and intentionally anti-aesthetic art, Marcel Duchamp's 'Fountain' (an ordinary urinal turned on its side), actually has a strikingly aesthetic design. For example, Duchamp's biographer Tomkins (1996) noticed similarities between the curves of the urinal and those of Brancusi's polished sculptures. As curvature is generally considered attractive (Gómez-Puerto et al., 2018), it is conceivable that part of the artistic success of 'Fountain' is inadvertently due to its aesthetic design. Furthermore, a urinal may elicit disgust, which has been shown to have a transmission advantage as well—even if the artwork is not liked (Jiménez & Mesoudi, 2019). Thus a cultural evolution perspective suggests that cultural success and persistence of art may be more closely linked to its (un)intentional aesthetics than commonly acknowledged by post-aesthetic philosophy of art.

Cultural Evolutionary Explanations

The two major cultural evolution research programs, cultural attraction and dual inheritance, have regarded art as involved in pivotal cultural evolutionary processes. Cultural attraction theory or the Paris program, pioneered by Dan Sperber, holds the view that culture gravitates towards particular forms due to attractors which can be various social, historical, or ecological factors, but most importantly, innate psychological factors (Milton, this volume; Sterelny, 2016). Sperber and Hirschfeld (2004) elucidate this view on cultural evolution by analogy with biological mimicry signaling. Harmless hoverflies evolved black and yellow stripes to mimic harmful wasps as a form of protection from predators. They thus exploit predators wasp detecting modules to their own benefit. Likewise, humans manipulate innate cognitive modules or predispositions of conspecifics to grab and direct their attention. Sperber and Hirschfeld (2004) assert that, for instance, the face recognition module has led to the massive cultural success of face-like stimuli such as masks, caricatures, and portraits, irrespective of whether these stimuli serve the original function of the module (i.e. whether they fall into its proper domain as real faces do).

Even though Sperber and Hirschfeld's (2004) comparison with biological mimicry implies that humans manipulate each others reactions via cultural forms ultimately to their own benefit, the Paris program does not generally consider such adaptive consequences explicitly, in line with its emphasis on cultural evolution as a proximate mechanism (Scott-Phillips et al., 2011). That is, according to the Paris program, culture is acquired (or reconstructed) during the lifetimes of individuals as part of development, rather than that it is evolved in the sense of naturally selected (see Figure 43.1).

However, since proximate and ultimate explanations are complementary, rather than alternative explanations of behavior (Laland et al., 2011), the Paris program view could arguably be regarded as complementary to standard evolutionary psychological hypotheses about art (see Figure 43.1). These hypotheses also often rely on signaling theory and propose, based on a number of similarities, that art

ultimately evolved as a signal to serve adaptive functions that generally occur in the animal kingdom. That is, one hypothesis proposes that art evolved, similarly to birdsong and bower decoration, as a sexual signal to attract mates (Darwin, 1871; Miller, 2000). Another hypothesis proposes that art, similar to primate grooming, evolved as a signal to foster within-group social bonds and group cohesion (Dissanayake, 1995). Still another one proposed that it evolved as a credible signal of quality to strengthen intergroup coalitions and defend territories, just as howling does in wolves (Hagen & Bryant, 2003; Hagen & Hammerstein, 2009). Others have noted that art may have been serving multiple of these signaling functions, just as, for example, birdsong does (De Tiège et al., 2021).

In contrast, dual inheritance theory, or the California program (Sterelny, 2016), pioneered by Robert Boyd and Peter Richerson, views cultural evolution as both a proximate and an ultimate process and is therefore a bit more radical in its ambition. The central idea here is that culture evolves fairly independent from genes, constituting a second inheritance system. Proponents assert that social transmission dynamics have been the primary drivers of human evolution, which amounts to what has been called culture-driven gene–culture coevolution (Richerson, Boyd and Henrich, 2010; Henrich, 2017) (see Figure 43.1). Major drivers of these dynamics are social learning biases, such as (anti)conformist, success, and prestige bias. They are seen as shortcuts, evolved to circumvent the fact that a given naïve learner by herself cannot assess which gradually accumulated cultural variants are adaptive and should be preferably adopted in a given environment (e.g. edible local flora knowledge) (Boyd & Richerson, 1985). Prestige bias, in particular, has gained much research attention (Offord & Kendal, this volume). It entails preferentially copying the cultural repertoires of prestigious individuals, whereby prestige serves as an indicator of covert cultural repertoire quality (Henrich & Gil-White, 2001; Jiménez & Mesoudi, 2019). Crucially, Boyd and Richerson (1985, p. 278) link it explicitly to the evolution of art and aesthetics, by analogy with runaway sexual signaling: ‘Much as peacock tails and bowerbird houses are thought to result from runaway sexual selection, the indirect [i.e. prestige] bias runaway process will generate traits with an exaggerated, interrelated, aesthetically pleasing but afunctional form.’

Note that on this view, aesthetics and art emerge in a coevolutionary process between learners and cultural models, and thus primarily from social learning dynamics rather than from converging to innate cognitive predispositions as the Paris program asserts. Boyd and Richerson (1985) discuss how several artistic traits may culturally evolve this way: tattoos, chants, clothing styles, elaborate symbolic displays, etc. Furthermore, Boyd and Richerson (1985, p. 278) note that ‘[i]f this hypothesis is correct, a large amount of cultural variation might be comprehensible only in terms of the internal logic that drove the runaway process in each culture’. Hence, just as sexual runaway has been argued to be responsible for much of aesthetic biodiversity (Prum, 2013), they argue that cultural runaway through prestige bias imitation behavior may account for cross-cultural human aesthetic diversity.

Intriguingly, humans’ heavy reliance on social transmission and the internal logic of social learning dynamics have been argued to have dominated human evolution to such an extent that the standard socio-biology/evolutionary psychology approach to human behavior does not suffice (Boyd & Richerson, 1985; Henrich, 2017; Laland & Brown, 2006; Richerson & Boyd, 2005). For instance, if mate choice exerts selection pressure on art, this view implies that its evolutionary history should be reconstructed differently than how evolutionary psychologists typically do. Based on the idea of culture-driven gene–culture coevolution (Richerson et al., 2010), Boyd and Richerson (1985, p. 278) argue that the cultural runaway process may entrain actual mate choice, such that ‘people may come to have genes that cause them to prefer mates who display a gaudy repertoire of cultural symbols. Perhaps the elaborate aesthetic sense of modern *Homo sapiens* is as much a consequence as a cause of cultural evolution.’ Despite this outspoken cultural evolution view on art and aesthetics, linked to

one of the most studied social learning biases (i.e. prestige bias), surprisingly few efforts have been undertaken to verify its predictions about art and aesthetics empirically.

In conclusion, despite their different emphases, evolutionary psychology, cultural attraction, and dual inheritance all essentially theorize about art based on models from signaling theory. This arguably offers underexplored opportunities for studying how the processes each of these programs deem fundamental are complementary versus contrasting. The following two sections attempt to flesh this out in some more detail.

Prehistory

While behavior does not fossilize, some of its material products may endure. The non-perishable traces of material cultures in the archaeological record allow us to investigate patterns over extensive time ranges. This also applies to art. As such, these material traces can be exploited to elucidate pending issues of cultural evolution, such as the causes and consequences of cultural stability and complexity, while also deepening our understanding of Palaeolithic art. This section deals with these matters based on the cases of the Acheulean hand axe and the Upper Palaeolithic emergence of figurative art.

The Acheulean is a symmetrical, teardrop-shaped hand axe. Based on its aesthetic design features that sometimes go beyond—or even against—its utility as a tool, it has been suggested to be a form of early art that might have evolved to attract mates (Kohn & Mithen, 1999). Archaeologists almost unanimously have assumed that the Acheulean industry is maintained by California program-style social learning and imitation (Corbey et al., 2016). However, its basic design displays surprisingly limited variability across Eurasia and Africa over roughly 1.5 million years. Richerson and Boyd (2005) do not consider it plausible that imitation-based cultural transmission alone could be responsible for such a spatiotemporally stable industry, especially, they argue, since traditions among the small semi-isolated groups of these early humans would have quickly diverged and variation between groups would have increased through time (but see a potential empirical counter-example of this in zebra finches: Tchernichovski et al., 2021). Instead, they contend that the Acheulean must have been constrained by some component of innate psychology. It is interesting to note that this in fact corresponds to one of the main tenets of Paris program-style cultural evolution, rather than their own California version. However, Richerson and Boyd (2005, p. 142) attribute this to the ‘relatively primitive imitative capacity’ of the producer of the Acheulean industry, *Homo ergaster*, in comparison to *Homo sapiens*. In so doing, they might imply that innate psychology would play a comparatively minor role in *Homo sapiens*. Yet, arguably, the cultural stability of the art of *Homo sapiens* seems to suggest otherwise.

In effect, albeit not quite on the same timescale (yet), *Homo sapiens* art traditions arguably display some patterns of remarkable spatiotemporal stability as well. Their iconography has been invariably dominated by large-sized animals (e.g. parietal art), and human figures (e.g. figurines), from about 45,000 years ago onwards, when undisputed figurative art appeared persistently in the archaeological records of antipodal regions of the world (Hodgson & Watson, 2015). Even in present times, both human and animal forms remain very popular themes in art (Verpooten, 2018). It seems plausible that this case of cultural stability is due to innate psychology as well, if only because it is consistent with animacy bias, an adaptive, highly conserved, cognitive mechanism that prioritizes visual attention to animal cues (including humans) (New et al., 2007).

So far, this all seems exclusively in line with evolutionary psychology and cultural attraction, rather than with dual inheritance. However, it is important to note that cultural stabilities, even if due to innate cognition, by no means preclude a crucial role for processes commonly associated with the dual

inheritance framework. This article considers two notable phenomena, the delayed appearance of Upper Palaeolithic figurative art and divergences from innate cognition in modern and contemporary art, in both of which social learning dynamics seem to play a key role. The remainder of this section deals with that delay, while the divergences are tackled in the next section. There is indeed a delay of about 100,000 years between the appearance of anatomically modern humans and complex artefacts such as figurative art in the archaeological record. While there have been attempts to attribute these appearances to innate psychology (i.e. genetically inherited neurocognitive changes; Mithen, 1996), this view has been contested by subsequent archaeological findings and is no longer accepted (McBrearty & Brooks, 2000).

A noteworthy alternative explanation has in effect been put forward within the California program of dual inheritance. This alternative draws on the relation between social transmission and demography. In evolutionary biology, the minimum viable population refers to the lower bound on population size to avoid extinction due to, for instance, genetic stochasticity. Analogously, it has been suggested that there is a lower bound on the interacting pool of social learners as well, required to maintain a particular level of cultural complexity. This lower bound exists for analogous reasons; that is 'to avoid' stochastic loss of unique cultural innovations and to ensure cumulative evolution, that is more (and more complex) innovations that are being maintained and built on top of each other (Henrich, 2004; Shennan, 2001). The size of the interacting pool of social learners or effective population size crucially depends on demographic factors, such as size, density, and interconnectedness of populations.

This general principle may apply to the specific problem of the late emergence of figurative art production as well. First, it has been argued that figurative rock art in effect displays several complex features that attest to reliance on cross-generationally accumulated innovations (i.e. skills, technical and material knowledge) (Verpooten & Nelissen, 2010). In contrast to technically much less difficult to make and comparatively much older abstract art (e.g. cross-hatchings), complex innovations such as shading in order to create three-dimensional illusions, processing of pigments, and marked stylization of depictions characteristic of figurative art tradition may not be retained if not for a sufficiently large effective population size (Verpooten & Nelissen, 2010). Furthermore, the fact that figurative art emerged fairly synchronously in antipodal regions of the world (Brumm et al., 2021; Hodgson & Watson, 2015) is consistent with evidence that a global supporting social network for cultural diffusion of relevant innovations was in place (MacDonald et al., 2021).

Second, evidence indicates temporal and geographic associations with relevant demographic parameters. Walker et al. (2021) demonstrate that parietal rock art has only become endemic in populations once a critical population density had been reached. It has also been argued that appearances of complex (including figurative) art indeed coincide with increases in size, density, and interconnectedness of populations (Powell et al., 2009; Verpooten & Nelissen, 2010).

Yet despite its explanatory potential, doubts have been raised about the validity of the demographic explanation, not only for the emergence of complex figurative art, but for cultural complexity in general. Collard et al. (2016) contend that ethnographic and archaeological data suggest that cultural complexity is most strongly influenced by environmental factors. Vaesen et al. (2016) propose a number of alternative explanations for complexity, namely population pressure, task specialization, and environmental risk, but admit those aren't without problems. In addition, experiments show that the need for intergroup communication may also cause art to become figurative (Granito et al., 2019), and this could perhaps provide an alternative (but also complementary) explanation for the association between mentioned demographic changes (i.e. increased interconnections between populations) and appearances of figurative art. Moreover, Acerbi et al. (2017) did not find a consistent relationship between population size and complexity in folktales, but they do suggest that this might be due to the

fact that narration is a non-technological domain—which is in contrast to visual art. Overall, these latter studies may suggest that there is more to cultural complexity than demography. Yet it should be noted that recent independent evidence in non-human animals does support the possibility that effective population size plays a significant boundary role, even in non-technological, aesthetic signaling domains such as birdsong cultures (Crates et al., 2021; Hudson & Creanza, 2022; Paxton et al., 2019). Hence, despite mixed results and attempts at rebuttal, effective population size remains a promising option for explaining particular patterns (at least boundary conditions) of cultural complexity.

In conclusion, this section aspired to show complementarity between evolutionary psychology, cultural attraction, and dual inheritance with respect to Palaeolithic art. One of the main argument was that while innate psychological predispositions may explain stability of figurative art, social transmission will likely be required to account for the timing of its emergence, persistence, and elaboration. The next section discusses how social transmission dynamics may even have a destabilize impact on art, in the sense that prestige bias social learning may pull it away from innate psychological predispositions. Thus, dual inheritance may extend standard evolutionary psychology and cultural attraction approaches in yet another way.

History

Albeit on a smaller timescale than prehistory, the more comprehensive historical record allows to investigate processes of cultural evolution of art in a more fine-grained fashion and shed light on its drivers in more recent times. Especially the Paris program has so far taken the opportunity to use art as a ‘fertile domain’ to study fundamental questions regarding cultural evolution empirically, commonly focusing on historical convergences to components of innate cognition (Miton et al., 2020). Two studies will be considered that exemplify this approach. Subsequently, experimental work will be discussed that aspired to integrate the Paris (cultural attraction) and California (dual inheritance) programs.

Morin (2013) investigated the gaze depicted in portraits from a cultural attraction perspective. Studies show that direct eye gaze catches the attention of adults and new-borns and that adults find it more attractive. Therefore, Morin (2013) expected that artworks exploiting this innate visual preference will be relatively more successful. Accordingly, he found that among sixteenth-century European portraits, direct-gaze paintings are more likely to be featured in today’s art books. He also showed that Renaissance portraiture evolved towards a strong predominance of direct eye gaze. Furthermore, these findings were replicated on a corpus of Korean portraits. Finally, he suggested that the shift in Renaissance portraiture was due to the gradual replacement of early painters by new generations of painters, who started their career by painting more direct-gaze portraits than their contemporaries, before the shift became tangible. Yet these painters came from different national and stylistic backgrounds and the fact that they were connected with each other by a series of pan-European visual revolutions (e.g. Mannerism) did not appear sufficient to explain the rise and sustained dominance of direct-gaze portraits. However, if the shift towards direct gaze is rather due to a pre-existing innate visual preference, the fact that both portraiture traditions initially diverged from it needs explaining as well. Morin (2013) provided such an explanation for the case of official Korean portraiture where, as court etiquette prohibited gazing directly at others, portraitists followed the same rule. But as soon as gaze direction is left free to vary, so that we find both averted and direct-gaze portraits, the latter style is expected to enjoy more success and, over time, become the default option.

Miton et al. (2020) also analysed a large dataset of portraits and similarly found that the influence of a plausible innate cognitive factor increased as a cultural norm was relaxed. Animals, including

humans, take advantage of the typical directionality of animal body plans. In observing other agents, it is generally the case, they argued, that what happens in front of them is more relevant than what might happen behind them. Miton et al. (2020) expected that this ancestral cognitive predisposition would cause a forward bias in the composition of profile portraiture. Accordingly, in a dataset of single-sitter human profile-oriented portraits produced by European painters between the fifteenth and the twentieth century it was found that these painters tended to put more free space in front of, rather than behind, the sitters. Secondly, in most of the period considered, there was a rather strong explicit cultural norm in favour of centring the sitter in the frame, which is in conflict with forward bias as this decentres the sitter. As expected, they found that the strength of forward bias increased when this cultural norm of spatial composition favouring centring became less stringent. Interestingly, Miton et al. (2020) reviewed evidence suggesting that while appreciators prefer the focal object (i.e. the sitters eye) decentred, producers tend to spontaneously centre it. This suggests that centring versus decentred forward bias may also be a question of production versus appreciation biases. This highlights the relevance of considering both signaler and reactor processes in art as in any signaling system (De Tiège et al., 2021).

Verpooten and Dewitte (2017) and Verpooten et al. (2023) also made explicit reference to cultural evolution theory, but they aspired to combine predictions from the Paris and California programs in their behavioral experiments. Verpooten and Dewitte (2017) asked art experts and non-experts to rate, as artworks, photo portraits depicting faces previously rated as either attractive or neutrally attractive. They told a random half of these participants, irrespective of their expertise, that the pictures belonged to the Museum of Modern art in New York (MoMA) collection and that it is one of the most prestigious museums in the world. The other half was not given such (false) information. Since facial beauty signals fitness and perceiving it is neuronally rewarding, artworks depicting them should appeal more to innate psychology. Thus, in line with the Paris program and evolutionary psychology, it was found that beautiful face portraits were preferred as artworks by non-experts (i.e. the general audience). It also did not matter to these non-experts whether the portraits were part of the prestigious MoMA collection or not. In contrast, experts preferred the portraits of neutrally attractive faces as artworks. Furthermore, when they were in the MoMA condition, they significantly increased their ratings of portraits compared to the experts in the control condition. These findings on experts are in line with the California program. That is, they are consistent with its prediction that prestige bias social learning may pull aesthetic preferences away from innate psychological predispositions (see section on cultural evolutionary explanations). In other words, expert art evaluation and judgement may be at least partially acquired through prestige bias social learning, which diverges it from innate psychological predispositions. Hence, overall, it appears that expertise acts as moderator of convergence towards innate psychology and prestige driven divergence from it (see Figure 43.1). As such, it may contribute to ongoing cultural evolution research on the relative importance of content biases (mostly due to innate psychology) and context biases (such as prestige) (e.g. Berl et al., 2021).

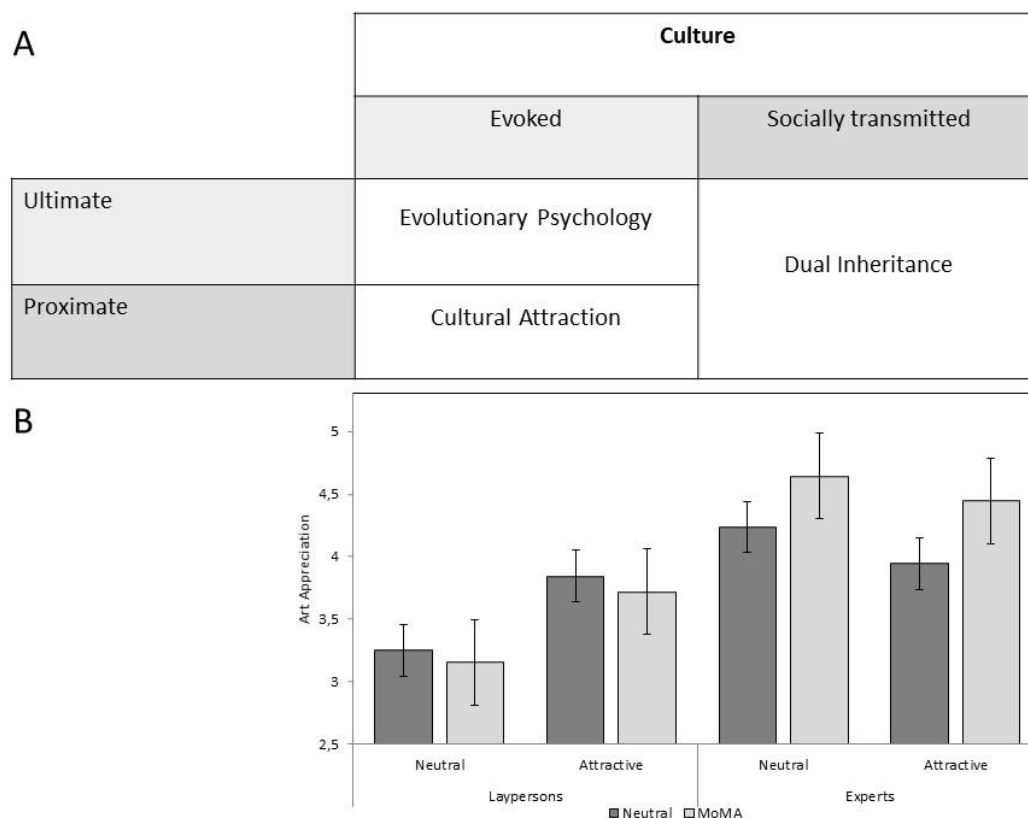


Figure 43.1

The table at the top (a) indicates the main focuses of evolutionary psychology, cultural attraction, and dual inheritance regarding conception of culture (evoked—transmitted) and level of explanation (proximate—ultimate). The figure below (b) from Verpooten and Dewitte (2017) highlights complementarity of these approaches with respect to art. That is, non-experts (the general audience) prefer artworks depicting beautiful faces over neutral ones, corresponding to an innate psychological predisposition (for facial beauty), consistent with evolutionary psychology and cultural attraction. Experts, on the other hand, are swayed by prestige context and diverge from this innate predisposition (preferring the neutral face pictures instead), consistent with the prestige bias cultural runaway process of dual inheritance.

Another study yielded similar results (Verpooten et al., 2023). A large sample of experts were again randomly distributed over a prestige (MoMA), and control condition. However, rather than facial attractiveness, here animacy depicted in artworks had been manipulated (i.e. inanimate objects such as a chair vs animate objects such as a pig). Again, an overall effect of prestige on expert ratings was found. Furthermore, as expertise increased, the effect of animacy on their art appreciation decreased. This happened to the point even that, at the highest echelons of expertise, depictions of inanimate objects were preferred over depictions of animals. As mentioned in the previous section, animacy detection and preference is a highly conserved component of innate psychology. Hence also, this study suggests, in line with the California program, that expertise and the use of prestige are associated with divergence from innate psychology (see Figure 43.1). The broader art-historical relevance of these experimental studies might be that they clarify the well-known schism between popular art and

entertainment on the one hand and high art on the other. That is, they suggest that popular art generally gravitates towards innate psychology of the general audience, while high art has coevolved with the evaluations of experts and ran away from popular art/innate psychology possibly due to the experts' use of prestige bias. At any rate, this prestige bias runaway model of high art is also consistent with a recent, extensive study (data on almost half a million artists) (Fraiberger et al., 2018). This study shows that current prestige of professional artists depends strongly on their prestige at the very start of their career as proxied by the prestige of the institutions that represent them. Artists that start at the periphery of reputational institutions face a mostly unsuccessful struggle for access to elite institutions (Fraiberger et al., 2018). Future research could verify whether similar processes occur in other cultural domains (e.g. sciences) as well. Given the current controversies surrounding the authority of experts more generally (Nichols, 2017), this is a timely topic to which cultural evolution research can contribute.

Both cultural evolution programs sometimes consider ecological factors (reviewed in Buskell, 2017), which could inform research into art as well. For example, obesity researchers found a spatiotemporal correlation between climate change and body size proportions of Upper Paleolithic Venus figurines, such that obesity decreased when the climate warmed and distance from glaciers increased. This was presumably in accordance with nutritional availability and perhaps insulation needs, which are especially relevant during pregnancy (Johnson et al., 2020). In that light it is interesting to note that the depiction of more voluptuous women seems to roughly coincide with the Little Ice Age in Europe culminating in the Rubenesque beauty ideal and the Maunder Minimum (the middle of the Little Ice Age).¹ It might indeed be interesting to check whether voluptuousness of more recent culturally successful depictions of (wo)men follow variations in caloric supply. For instance, is it coincidental that the beauty ideal of Marilyn Monroe, which is a bit more voluptuous than before and after the 1950s, co-occurs with a drop in caloric supply due to the Second World War? Or that the extremely thin heroin-chic beauty of ideal of the 1990s lasts until about 2000, when caloric supply peaked?

Overall, the empirical findings and methods discussed in this section and previous sections are complementary and can play even synergetic roles in future research. Analysis of historical datasets could be complemented with relevant behavioral experimentation. For example, it might be verified whether eye-gaze direction has an expertise-dependent influence on appreciation of portraits as well. In addition, in order to overcome the limitations of preference studies, future research should also attempt to measure transmission more directly using experimental paradigms such as transmission chains (Jiménez & Mesoudi, 2019). This could also be combined with algorithms designed to evaluate more subtle and complex changes in large historical databases. For instance, using this method, it was found that trustworthiness as expressed in European portraits increased in the last 500 years in parallel with the decline of interpersonal violence and the rise of democratic values (Safra et al., 2020).

A final research strand increasingly worthy of close attention due to new advancements and promising prospects is the cross-species comparative analysis of relevant aspects of cultural evolution of art and aesthetics.

Cross-species Comparison

Often reference is made to other species when discussing particular issues in cultural evolution. Similarly, a more systematic comparative approach to the cultural evolution of art and aesthetics is called for as well. This should entail a cross-species investigation of proximate (development and

¹ The author thanks Pieter Theuns for this suggestion.

physiology) and ultimate (phylogeny and function) aspects of relevant components such as creativity, artifactuality, aesthetics, and social transmission (cf. Fitch, 2006; cf. Seghers, 2014, 2016). Such analyses could also solve the particularly intriguing puzzle as to why humans appear to have aesthetic cultures in common with genetically distantly related taxa, such as birds, bats, and whales, but not with more closely related primate relatives. While this absence among non-human primates complicates phylogenetic reconstruction, solving it would arguably clarify the hurdles humans overcame to unleash their artistic capacities.

Animal aesthetic culture usually refers to cross-generationally socially transmitted signals that evolved to manipulate neuropsychology of conspecific receivers and/or that have coevolved with their evaluations (Prum, 2013; De Tiège et al., 2021). Common examples include humpback whale, oscine songbird, parrot and hummingbird song cultures, and the various bowers, constructed and meticulously decorated by bowerbirds (Diamond, 1991; Prum, 2013). In contrast, no indication of substantial aesthetic culture has been reported in non-human primates. While some primates are said to sing, none of them is capable of vocal imitation required for the evolution of song cultures (Verpooten, 2021), and while great apes are avid nest builders and tool-makers, capable of sophisticated motor learning and maintenance of material cultures, these capacities have not been recruited for elaborate aesthetic signaling (except perhaps under guidance by humans in captivity) (Verpooten & Joye, 2014). Thus, any explanation for the evolution of art and aesthetics in the human lineage should pass the chimp test: it must explain why we find little evidence for aesthetic culture in non-human primates like chimpanzees, genetically close to humans, while we do seem to find it for distantly related taxa.

This suggests that ecology should be considered as well. For example, it has been argued that the greater observed creativity of great apes in captivity has to do with reluctance to be creative in the wild due to predation risk and the need to remain vigilant. Only when early humans became ecologically dominant (apex predator-like), and therefore virtually immune to predation, could they become creative (van Schaik et al., 2016). A similar explanation has been invoked for the absence of vocal imitation capacity in several taxa (Jarvis, 2006). It has also been put forward that species with plenty of 'leisure time', such as humans and bowerbirds, due to, primarily, their foraging efficiency, can 'channel it [i.e. time] into more lavish [art-like] signals to outdo each other', whereas species with little spare time, such as chimpanzees, cannot (Diamond, 1991). Another hypothesis focuses on the apparent association between the evolution of aesthetic culture and the three dimensionality of the environment (six out of eight taxa of complex vocal learners, corresponding to more than 99 per cent of species, inhabit aerial and aquatic environments; Verpooten, 2021). This may be due to the fact that in three-dimensional mating environments, male coercion and defence of territory against rivals are not effective strategies and that therefore females can exert more selective pressure on males to signal covert information such as genetic quality through ornaments and aesthetic displays, including culturally transmitted ones (e.g. bowers and song cultures) (Pradhan & van Schaik, 2009; Puts, 2010; Verpooten, 2021).

Recent advances in phylogenetic comparative methods create new opportunities to systematically investigate relevant aspects of cognition, behavior, ecology, etc. across large and relevant swathes of the phylogenetic tree. Such analyses could elucidate the puzzling taxonomic distribution of aesthetic cultures.

Conclusions

This article has primarily focused on the differences and overlaps between evolutionary psychology, cultural attraction and dual inheritance approaches to art. I argued that these research programs are

largely complementary and that synergies can be accomplished by realizing that they are based in specific but complementary models within the more general and unitary framework of signaling theory. Specifically, evolutionary psychology and cultural attraction studies have demonstrated the existence of innate cognitive predispositions (e.g. animacy, eye-gaze, facial beauty), and cultural convergences towards these predispositions, respectively. In addition, consistent with dual inheritance, experiments on art appreciation suggest that prestige bias social learning may pull art preferences away from these predispositions. Furthermore, also consistent with dual inheritance, social transmission and accumulation of innovations seems a requirement for figurative art, in correspondence with its appearances in the archaeological record and demographic aspects. This article also highlighted that ecological factors and cross-species comparative data should be taken into account as well. Factors such as predation risk or dimensionality of the environment may account for the fact that humans share aesthetic cultures with distantly related vertebrate taxa such as whales, parrots, and songbirds but hardly with non-human primate relatives. Taken together, different methods, insights and theoretical approaches across a diverse range of disciplines, several of which have been touched upon in this article, are painting an increasingly cogent picture of the cultural evolution of art.

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