

An Evolutionary Approach to Art and Aesthetic Experience

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A comprehensive characterization of the neurobiological underpinnings of artistic activities and aesthetic experience will require understanding of their evolution. Evolutionary approaches to these phenomena have thus far lacked adequate conceptual, archaeological, and neurobiological grounding. Here, after the necessary conceptual clarifications, we review the basic archaeological and neurobiological evidence that should be accounted for by any hypothesis about the evolution of visual art and aesthetic appreciation. We end by arguing that, in order to overcome the limitations of prior interdisciplinary attempts, such scenarios should take the form of gradual and mosaic coevolutionary processes.

Keywords: brain, beauty, paintings, evolution, archaeology

Humans spontaneously produce widely varied aesthetic artifacts, understood as objects experienced perceptually on a continuum from the pleasant to the unpleasant. This includes objects humans enjoy looking at, listening to, smelling, touching, or tasting, as well as those with which they do not enjoy engaging. In the sense that humans are capable of such aesthetic orientation toward artifacts around them, as well as natural elements and phenomena (e.g., scenic views, sunsets, faces), they may be unique as biological organisms. Some of these aesthetic objects are created as part of a given society's artistic tradition, though much art around the world is created with no concern for aesthetic issues. Art has been defined as the turning of an object (such as a painting, sculpture, or centerpiece) or activity (a dance, ceremony, or meal) into something special (Dissanayake, 1992, 2000). It is thus a domain of human experience that is different from aesthetics, though both have overlapped at certain points in discussions (Shiner, 2001). Art is ubiquitously produced throughout the world where human societies exist and has taken on wide forms of expression (Dissanayake, 1992, 2000; Dutton, 2009). One of neuroaesthetics' main objectives is to characterize the neural underpinnings of such varied artistic activities and aesthetic experiences. This endeavor, however, also requires understanding the evolutionary history of the crucial neural systems: how, when, and why did they come into place (Zaidel, 2005). Both lines of inquiry are intrinsically related, yet work on the neural correlates of art and aesthetics has generally been carried out with no evolutionary concerns, and hypotheses about the evolution of art and aesthetics have been put forward with virtually no neuroscientific or archaeological backing.

This is not the only case of inefficient interdisciplinarity within the field of neuroaesthetics. Croft (2011) has shown that misunderstandings between humanists and scientists, misapplication of each other's findings and concepts, and reduction of each other's complex notions to the point of rendering them vacuous can be found even in high-profile contributions to the field. One of the problems that hampers interdisciplinary progress in neuroaesthetics is the way scientists have used important concepts, such as art and aesthetic experience, out of their humanist contexts and without taking into account their particular historical background.

In this article, we bring together crucial archaeological and neurobiological evidence that any approach to the evolution of art and aesthetic appreciation should account for, and we offer a general characterization of this process, while attempting to meet the disciplinary standards of the relevant fields: art theory, philosophical aesthetics, psychology, neuroscience, and archaeology. For practical reasons, we focus on visual manifestations of art and aesthetics, though our views easily extend to many other kinds.

Art and Aesthetics

Our current understanding of art and aesthetic experience—neuroaesthetics' main objects of study—owe a great deal to 18th century European philosophers. They shaped our common notion of artworks as autonomous objects devoid of all function and created to be experienced aesthetically. This separation of art from other spheres of human life, which is uncommon in other cultures around the world, was accompanied by the disconnection of aesthetic experience from all usefulness and everyday pleasure (Carroll, 2008). Art, before then, had traditionally served people's social, moral, religious, and recreational interests, as it still does in many nonwestern societies (see Dissanayake, 1992). Yet, during the 18th century, the enjoyments of sight and sound were given a greater intellectual weight, separating them from the so-called lower and sensual pleasures. Thus, disinterested contemplation became the appropriate way for polite people to approach art (Shiner, 2001) and a central concept in many philosophical approaches to aesthetics, though it has certainly been challenged on several occasions (e.g., see Shusterman, 2005).

If neuroaesthetics aspires to contribute meaningfully, it must be able to account for varieties of art and aesthetics across many

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human cultures, as well as recognize that art is not the only source of aesthetic reactions, as noted previously (e.g., Zaidel, 2005; Brown & Dissanayake, 2009). Nonwestern art is often performed and enjoyed as an intrinsic element in rituals, celebrations, ceremonies, and many other events, and the associated experiences serve several purposes, such as economic, social, political, or symbolic. Likewise, aesthetic concerns in nonwestern cultures generally permeate a broader range of activities and objects and are related to the communication and experience of spiritual, ethical, and social meaning (Anderson, 1989; Dissanayake, 1992). There are, in fact, for humans numerous sources of aesthetic experiences including, nature scenery, food, music, faces, smells, and many more. The fact that art does not constitute the sole source of aesthetic reactions suggests a biological ancestral origin for these reactions (Zaidel, 2009).

Thus, neuroaesthetics needs to explain the evolution of the neural mechanisms that endowed humans with the capacity for production of visual, auditory, olfactory, gustatory, tactile, and kinesthetic experiences. These products and experiences might be associated with the beautiful, the ugly, the comic, and the symbolic, as well as identity, and so on. People can adopt a disinterested attitude toward them, but also show considerable degrees of interest, expressed in the forms of liking or disliking, wanting or rejecting, accompanied by colorful affective and emotional experiences. We will thus use the terms art and aesthetics in the broad and inclusive sense noted in the first paragraph of this article, though we understand that some may argue that this is overstressing their conceptual boundaries.

The Archaeological Evidence

To reach a deep understanding of the neuroscience and psychology of art, we need to ask at what point art practice first appeared in the ancestral lineage of the *Homo sapiens*. Paleoanthropologists usually regard this kind of archaeological remains as part of a broad set of indicators of modern human behavior, together with innovations related with technology (microblades, hafting, and the use of bone and antler to craft tools), economic and social organization (long-distance exchange networks or specialized hunting), and ecology (broadened diet) (McBrearty & Brooks, 2000).

There are two opposite explanations for the origin of behavioral modernity. The “revolution hypothesis” sees evidence in the archaeological record for a recent and fast appearance of modern human behavior in Europe about 40,000 years ago. The richness of European Upper Paleolithic remains, which contrasts with evidence from Middle Paleolithic sites indicating lower effectiveness in resource exploitation and simpler and less varied technology, (with few markers for symbolic behavior), is taken as evidence for a substantial change in human cognition (Mellars, 1991) and possibly its underlying neural systems (Klein, 1995).

The “gradualist hypothesis” argues that not all the behaviors characterized as modern arose at the same time and place. Evidence for an early visual culture by way of beads, line engravings in chunks of pigmented ochre, or purposeful markings on ostrich egg shells, has been found in South Africa, in the Blombos Cave, and dated to around 75,000 years ago (Culotta, 2010; d’Errico et al., 2003; d’Errico, Henshilwood, Vanhaerend, & van Niekerk, 2005; Henshilwood, d’Errico, & Watts, 2009). Several scholars have suggested that the intention of the pigments, purposeful

markings, and shell beads was to signal personal identifiers; before image making began (drawings, paintings, and so on), body ornamentation was used to signal belongingness to a group or subgroup (Henshilwood et al., 2009). We do not wish to enter the futile controversy as to whether such artifacts are, in themselves, symbolic. However, following Henshilwood and Marean (2003) and Zilhão’s (2007) conclusion that the capacity for symbolic expression can be inferred “when artifacts or features carry a clear symbolic message that is exosomatic—for example, personal ornaments, depictions, or even a tool clearly made to identify its maker” (Henshilwood & Marean, 2003, p. 644), we believe that the archaeological context in which the finds were made together with the ecological and cultural context of the aforementioned findings suggest that they constitute undoubtable expressions of symbolic cognition. There is evidence for earlier use of symbolic cognition as well, notably from Israel, dating to about 100,000 years ago (Bar-Yosef Mayer, Vandermeersch, & Bar-Yosef, 2009), and there is evidence from Africa dating to even earlier times (McBrearty & Brooks, 2000). McBrearty and Brooks (2000) have strongly argued that European Upper Paleolithic archaeological evidence is the result of a gradual and continuous accretion of novel behaviors over a long period of time.

Pigments, for instance, have been used quite commonly in Africa for more than 130,000 years (Barham, 2002; Henshilwood et al., 2011; Marean et al., 2007). Barham (2002) described a set of more than 300 pieces of mineral pigments covering a broad palette of yellow, brown, red, purple, pink, and dark blue colors at the 200,000-year-old site of Twin Rivers (Zambia). Given that these kinds of minerals can be used for making glue for hafting (Wadley, Hodgskiss, & Grant, 2009), researchers believe that additional evidence is needed to prove that pigments were used for symbolic purposes. One example is the choice of a reduced palette, as with the highly prevalent reddish-brown pigments at the 164,000-year-old Pinnacle Point site in South Africa (Marean et al., 2007) and the specifically red hues at Qafzeh Cave in Israel, dated to 90,000–100,000 years (Hovers, Ilani, Bar-Yosef, & Vandermeersch, 2003). An even more compelling indication that pigments had purposeful (symbolic) intention is the presence of crisscross lines engraved in pieces of red ochre retrieved at Blombos Cave, in South Africa (Figure 1, a–c), dated to between 75,000 and 100,000 years (Henshilwood et al., 2002; 2009).

Similar pieces, dated to between 80,000 and 50,000 years ago, have been found at the Klein Kliphuis rock shelter (South Africa). Notably, they are associated with tools belonging to a different and more recent technological complex, suggesting that the tradition of engraving on ochre might extend past technological barriers. Parallel and crosshatched engravings were also made on bone (Figure 1d) and ostrich shells (see Figure 2) in South Africa between 70,000 and 60,000 years ago (d’Errico, Henshilwood, & Nilssen, 2001; Texier et al., 2010). In all of these finds, symbolic cognition is inferred not only from markings on ochre or bones or from presence of pierced beads but from the entire context of all the findings in the archeological site.

There is also ample evidence for personal ornamentation outside of Europe long before the Upper Paleolithic. The shell beads in Blombos Cave date to 75,600 years ago (d’Errico, Henshilwood, Vanhaerend, & van Niekerk, 2005). Notably, these were selected for their large size, were transported for more than 20 km, and were perforated at the lip, strung together, and worn for long

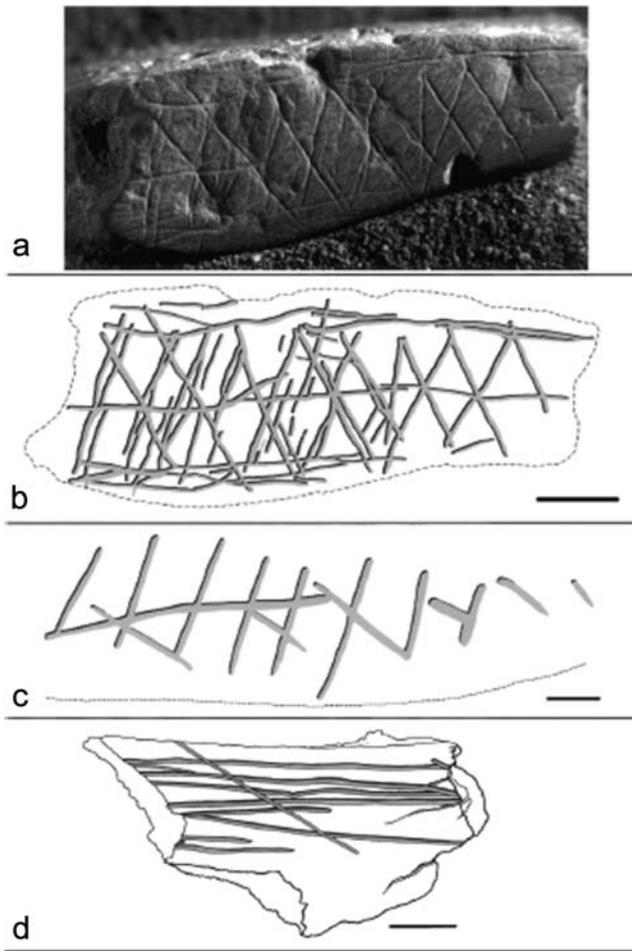


Figure 1. Abstract engravings from Blombos Middle Stone Age levels. (a–c) Photo and tracing of engraved patterns on the edge of ocher slabs; (d) tracing of an incised bone fragment. (b) Scale D 1 cm, (c) scale D 2 mm (d) scale D 5 mm. Taken from d’Errico and colleagues (2003), with kind permission from Springer.

periods. Residues indicate that they were either painted or rubbed against other colored items, such as clothes, or even bodies. Similar evidence of seashell selection, transportation, stringing, and pigmentation has been retrieved from Skhul (dated to 100,000–135,000 years) and Qafzeh Cave (95,000 years) in Israel, Oued Djebbana (older than 35,000 years) in Algeria, and several sites (between 75,000 and 85,000 years old) in Morocco (Bouzouggar et al., 2007; d’Errico et al., 2009; Hovers et al., 2003) (see Figure 3). Beadwork, therefore, was common across Northern Africa and the Levant before modern humans arrived in Europe (Vanhaeren et al., 2006). Intriguingly, though, this intense use of shell beads for personal ornamentation seems to have become obsolete after 70,000 years in Africa and the Near East (d’Errico et al., 2009).

The first humans to reach Australia, between 44,000 and 50,000 years ago, almost certainly engaged in art-related behaviors, such as personal ornamentation and the transportation and processing of ochre (Balme, Davidson, McDonald, Stern, & Veth, 2009; Davidson, 2010). Different regional styles of engraving and painting are

observable even at the very earliest stages of the Australian colonization, producing geographically and chronologically distinct records throughout the duration of human occupation of the continent (Davidson, 2010).

The Australian regional variation shows that modern humans did not express their cognitive capacities as a uniform set of behaviors (Brumm & Moore, 2005). The same can be said of both the African and the large body of the European Upper Paleolithic archaeological records. Conkey (1987) has argued that referring to such archaeological evidence as art has caused technically and contextually diverse manifestations, separated by thousands of kilometers and tens of thousands of years, to be misleadingly lumped into a single category. Moreover, art is a culturally bound category; it hoodwinks us into considering these objects as aesthetic manifestations and viewing them as the beginning of the history of our art. It is not possible to account for all these archaeological remains with a single explanation (Nowell, 2006), let alone one that is so culturally contingent as the Western ideal of art and aesthetics.

Symbolic cognition (following the aforementioned definition provided by archaeologists, which is intimately associated with modern human behavior) is seen as a critical prerequisite for the production of art, because art is referential and representational. Such abstract cognition is the hallmark of the human mind compared to other animals. One commonly discussed example of symbolic cognition is human language, which is considered the most sophisticated of all communicative systems in the biological world. With its vocabulary and syntax, human language affords an infinite number of combinations that convey a flexible range of meanings. However, language is not the only reflection of symbolic communication practiced by humans. Ideas and concepts forming in the mind become represented referentially in art works as well, whether in coloring arrows or parts of the body; in drawings, paintings, music, dance; or in stringing seashells into a necklace (to serve as markers and identifiers of the wearers). That is not to say that all art has symbolic value; some is purely decorative and emotionally arousing, for example. However, it is critical to keep in mind that art is produced in a brain whose hallmark is abstract, symbolic cognition. Like human language, the artistic combinations humans have constructed are now infinitely varied. Indeed, art is a communicative system that conveys myriads of ideas, metaphors, symbols, concepts, and emotions within the originating culture as well as universally (Zaidel, 2005, 2010).

Although abstract (symbolic) cognition is probably at the core of these manifestations, other important events and conditions have contributed to the eventual habitual practice of art by human societies. Specifically, climatic conditions, food resources, and genetic influences notwithstanding, the roles of both the social group size and culture are viewed now as major contributors to the enhancement of art-related practices (Bowles, 2009; Culotta, 2010; Mace, 2009; Wadley, 2001; Zilhão, 2007) and are key to understanding the archaeological record’s pattern and variability (Nowell, 2010), even in its European Upper Paleolithic exuberant expression (Mellars, 2009). This European creative explosion took place approximately 150,000 years after the acquisition of abstract cognition by the early *H. sapiens* (McBrearty & Brooks, 2000), and, furthermore, as noted by Renfrew (2009), it was intense and localized, only one of several similar episodes during our species’ history. Each of them occurred in a particular context and exhibits distinctive features.

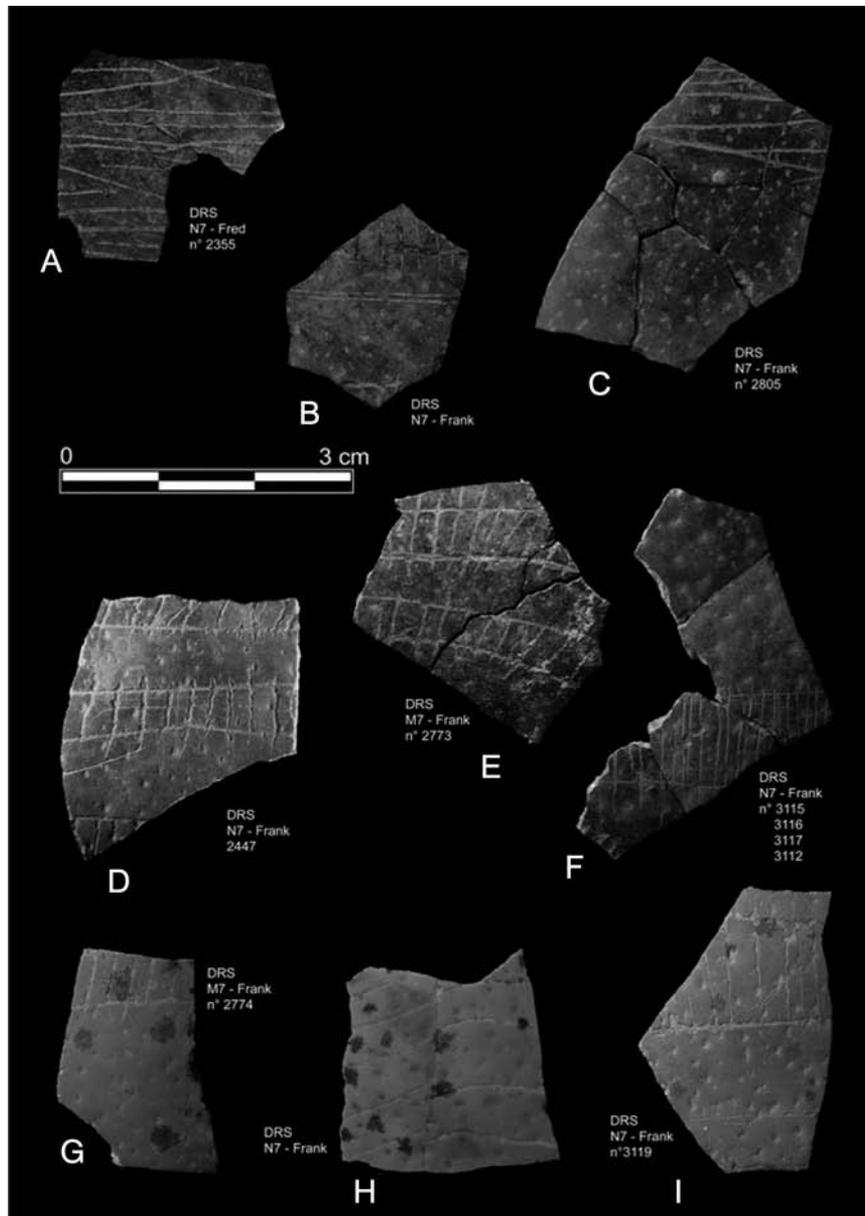


Figure 2. Fragments of engraved ostrich eggshells retrieved at Diepkloof Rock Shelter, Western Cape, South Africa (Teixer et al., 2010). All were located in the same stratigraphic unit, except for fragment A. Fragments A and C were engraved with straight, almost parallel lines. Fragments B, D, E, F, G, and I exhibit a hatched band motif. There is evidence on fragments B and E of two separate hatched bands. Fragment D presents three different bands. Fragment H was engraved with slightly curved lines crossing a central vertical line. By courtesy of Pierre-Jean Teixer.

The Neurobiological Evidence

There are two major sources of data on the underlying brain mechanisms of art and aesthetics. One is based on inferences drawn from the behavior of professional artists with brain damage and one is the data collected with normal participants in functional imaging studies. From the former we have learned that artistic productions can continue despite extensive damage to the brain, and importantly, regardless of the etiology, later-

ality, or localization of the damage (Zaidel, 2005, 2009). Moreover, there is remarkable paucity of reports of neurological cases with a reversal of aesthetic sensibility following damage to the brain. This suggests a stable and consistent neural representation of aesthetic reactions, one that lacks a specific center or pathway.

From neuroimaging studies we have learned quite a bit. Neuroscience research has focused on pinpointing the brain structures and pathways associated with aesthetic reactions (Brown, Gao,

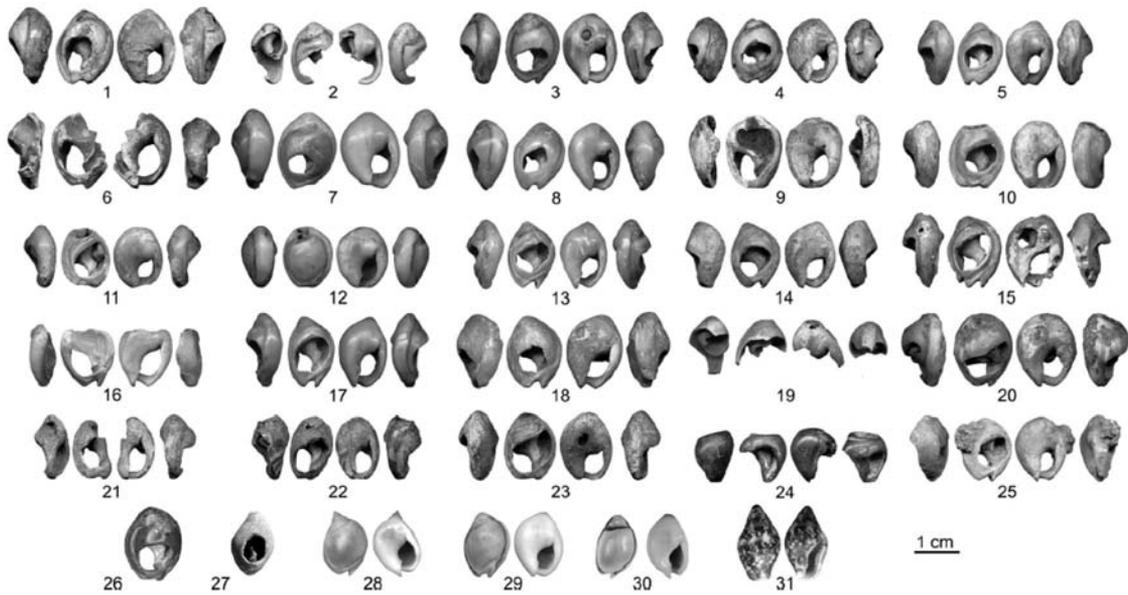


Figure 3. Marine shells used as beads found at Moroccan Middle Paleolithic sites (d'Errico et al., 2009). Shells 1–19 are from Taforalt (Grotte des Pigeons); Shells 20–24 are from Rhafas; Shell 25 is from Contrebandiers; Shells 26 and 27 are from Ifri n' Ammar; Shell 28 is a modern *Nassarius gibbosulus*; Shells 29 and 30 are modern *Nassarius circumcinctus*; Shell 31 is a modern *Columbella rustica*. By courtesy of Vanhaeren and d'Errico (the photographers).

Tisdelle, Eickhoff, & Liotti, 2011). Thus far, such studies have typically depended on an explicit behavioral aesthetic reaction as measured in a rating scale. The assumption is that aesthetic experience can be quantified with explicit reactions, that such measures can capture the essence of the aesthetic experience, and that they do not, in fact, interfere with it. Like all explicit behavioral measures, rating scales have their limitations. The extent to which explicit beauty, liking, or preference ratings alone can reliably capture the essence of aesthetic experience remains to be determined. In the absence of better tools, at the moment rating scales are viewed as reasonable measures. In the future, implicit measures such as the physiological response known as the Galvanic Skin Response (assesses imperceptible sweat on finger tips) should be added.

Taking this under advisement, the results of several neuroimaging studies suggest that brain activity underlying aesthetic appreciation of music, painting, architecture, or sculpture is associated with three kinds of processes (Nadal & Pearce, 2011) (see Figure 4). First, aesthetic experiences appear to rely on reward value representation, linked to activity in the orbitofrontal cortex (Blood & Zatorre, 2001; Cupchik, Vartanian, Crawley, & Mikulis, 2009; Kawabata & Zeki, 2004; Kirk, Skov, Christensen, & Nygaard, 2009; Kirk, Skov, Hulme, Christensen, & Zeki, 2009), the interaction between cognitive and emotional processes, as suggested by activity in the insula, temporal pole, and ventromedial prefrontal cortex (Brown, Martinez, & Parsons, 2004; Cupchik et al., 2009; Jacobsen, Schubotz, Höfel, & von Cramon, 2006; Kirk, Skov, Hulme, et al., 2009; Koelsch, Fritz, von Cramon, Müller, & Friederici, 2006), the monitorization of one's own affective state or conflict resolution, associated with activity in the anterior cingulate cortex (Brown et al., 2004; Cupchik et al., 2009; Kirk, Skov,

Christensen, et al., 2009; Vartanian & Goel, 2004), and the generation of pleasant and unpleasant feelings in anticipation and response to rewarding stimuli, as interpreted from the involvement of subcortical components of the reward circuit in aesthetic experiences (Bar & Neta, 2007; Blood & Zatorre, 2001; Brown et al., 2004; Cupchik et al., 2009; Kirk, Skov, Christensen, et al., 2009; Koelsch et al., 2006; Vartanian & Goel, 2004). Second, neuroimaging studies have identified an enhancement of cortical sensory processing in bilateral fusiform gyri, angular gyrus, and the superior parietal cortex (Cela-Conde et al., 2009; Cupchik et al., 2009; Vartanian & Goel, 2004) during visual aesthetic experiences, primary and secondary auditory cortices during musical aesthetic experiences (Brown et al., 2004; Koelsch et al., 2006), and the extrastriate body area of the occipital cortex and the ventral premotor cortex during aesthetic appreciation of dance (Calvo-Merino, Urgesi, Orgs, Aglioti, & Haggard, 2010). Third, high-level top-down processing and activation of cortical areas involved in evaluative judgment, such as the dorsolateral and medial prefrontal cortices, have also been shown to accompany aesthetic experiences (Cela-Conde et al., 2004; Cupchik et al., 2009; Jacobsen et al., 2006).

It is commonly assumed that because artistic activities appeared after humans and chimpanzees diverged, we must trace their evolutionary ancestry strictly within our lineage (Miller, 2001). However, all the aforementioned brain regions, whose activity is believed to sustain aesthetic experiences, are involved in innumerable other kinds of experience. This suggests that artistic and aesthetic activities rely on nonspecific neural mechanisms, which might even be shared with some of our close primate relatives, despite the fact that they do not produce anything closely resembling art. In fact, in addition to some relevant differences, com-

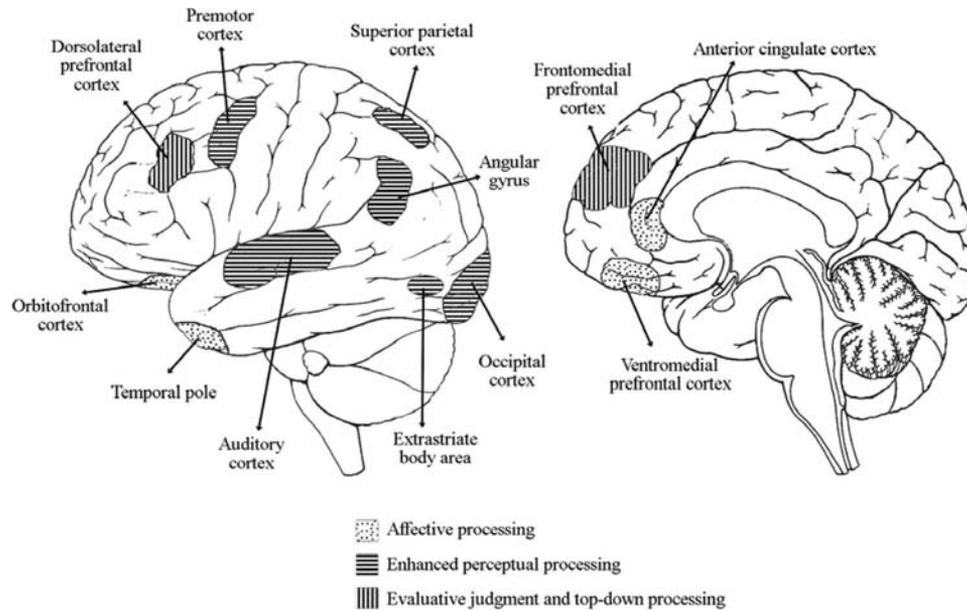


Figure 4. Cortical brain activity associated with aesthetic appreciation.

parative neuroanatomy has revealed extensive parallels among human and nonhuman primates in the cytoarchitecture and connectivity of brain regions involved in aesthetic experiences (Nadal, Capó, Munar, Marty, & Cela-Conde, 2009).

These commonalities refer to aspects of the cytoarchitecture and functions of the lateral, anterior, and orbital prefrontal cortices and the temporal poles and the retinotopic organization of primary and secondary visual areas, as well as the representation of objects and the processing of symmetry (Bell, Hadj-Bouziane, Frihauf, Tootell, & Ungerleider, 2009; Leichnetz, 2001; Orban, Van Essen, & Vanduffel, 2004; Petrides & Pandya, 1999, 2001; Semendeferi, Armstrong, Schleicher, Zilles, & Van Hoesen, 1998, 2001). Such similarities suggest that these features have not been significantly altered and were not under strong selective pressure during human evolution.

On the other hand, certain features of the neural systems known to be involved in aesthetic experiences show clear evidence of having been modified during human evolution. Specifically, multimodal association cortices have enlarged, the connectivity between and within prefrontal regions has increased, prefrontal cortices seem to process information from a broader range of sensory modalities, the cytoarchitectural organization of the anterior cingulate cortex has been significantly reconfigured, the dorsal visual stream has been expanded and elaborated, and the basal ganglia have expanded, developed an increased internal regulation, and receive greater inputs from the orbitofrontal cortex and anterior cingulate cortex (Amiez, Joseph, & Procyk, 2005; Denys et al., 2004; Holt, Graybiel, & Saper, 1997; Leichnetz, 2001; Nimchinsky et al., 1999; Orban et al., 2004; Semendeferi et al., 1998, 2001). These evolutionary developments probably afforded humans the capacity to produce abstract representations that are not necessarily tied to sensory modalities or associated with real entities, that is, symbols, an enhanced supervision of information processing and conflict monitoring and resolution, a sophisticated

processing of visual spatial relations, and an increased regulation and self-awareness of affective and emotional states.

Hence, we inherited some of the basic constituents of the neural networks that currently underlie aesthetic experiences from our distant primate ancestors, suggesting that the evolutionary history of some of the neural mechanisms that support such experiences even predates the appearance of hominins. However, specific alterations to certain brain regions involved in our capacity for aesthetic experience, which allowed an increased integration and elaboration of information and an enhanced regulation of our cognitive and affective processes, were fixed by natural selection in the particular course of human evolution. Given the distributed nature of the neural networks under discussion, it is unlikely that there has been a single evolutionary event that altered them, but rather, gradual changes throughout the human lineage, and probably owing to diverse selective pressures.

Moreover, evolutionary adaptive modifications to this neural network were surely not only relevant to this domain; all of the brain regions discussed here are involved in a number of other human cognition and behaviors as well. Hence, it is reasonable to assume that some brain modifications leading to our capacity to perform aesthetic valuations were not selected for the advantages conferred by it. Shared brain regions for several forms of cognition is a likely possibility (Zaidel & Nadal, 2011).

Evolutionary Mechanisms

The evolutionary mechanisms related to art itself and the aesthetic reactions to art have also been linked to our biological ancestry, specifically to procreation and mate selection strategies (Miller, 2001, 2009; Volland & Grammer, 2003; Zahavi, 1978). In the biological world procreation is key to the survival of the species, and mating is critical (Cronin, 1992). Organisms have developed widely varied and sophisticated means to attract a mate

in order to produce a viable offspring (Gould & Gould, 1989). In the great majority of species, the males use elaborate displays with the aim of attracting a female. The displays are intended to exhibit skills, prowess, survival abilities, health status, and above all, fitness and genetic quality. According to Darwinian principles of survival, females would prefer mating with males who possess the highest marks in these areas, on the (unconscious) biological assumption that her offspring will inherit superior qualities and hence survive better than those whose mothers made poorer choices of mates (Darwin, 1871/1998). The female's assessment is said, in Darwinian terms, to drive the development of the various male displays and exhibits.

Generalizing to art, the display of art has been compared to displays of fitness qualities in nature (Miller, 2001; Zahavi, 1978), and the aesthetic reactions to the art to emanate from activation of brain pathways associated with assessment of fitness quality exhibited in the display. In this scenario, to use the classic example, the peacock's display of its tail is akin to the display of human art, and the peahen's reaction akin to our aesthetic reactions (Zaidel, 2010). Our aesthetic reaction is to the talent, skill, creativity, innovation, intellectual, and virtuosity we detect in the art. In both cases, communication occurs between the producer (the peacock or the artist) and the observer (the peahen or the audience). The peacock communicates biological information to the would-be female mate through the majestic fanning of its tail, vibration of the upright fan, and back-and-forth struts in front of her; from these cues, the peahen is able to assess his strength, skills, and fitness. The exhibit of abilities and qualities is common to mate selection strategies and to humans displaying art.

We do not know how aesthetics factor into the peahen's choice of a mate. Elements of what we consider aesthetics could turn out to be part of her mental formula in making the choice. In humans, we do know that aesthetics play a role in assessing artworks, and we assume a biological origin for it that is associated with pleasure, and, here, too, we do not know whether the peahen derives pleasure from assessing or viewing her peacock's display.

Although the issue of pleasure and aesthetic reactions are often paired in scholarly discussions, aesthetics and art require further fine tuning with respect to origins: Given human symbolic and abstract cognition, and the uniqueness of art production in human societies, we should assume that aesthetic reactions to art are humanly unique, too, and are couched in the same type of abstract cognition. Thus, although aesthetic-related experiences are triggered by sources such as nature scenery, food, or faces, those experienced in relation to art activate additional neural pathways. The view we propose here, then, is that all aesthetic-related reactions in humans have biological origins, which activate processes shared with our biological ancestry, whereas the additional ones have evolved adaptively to match the symbolic and abstract cognition expressed in art.

The Evolution of Art and Aesthetic Experience: A Preliminary Sketch

The evidence reviewed above might not be enough to provide a detailed account of the evolution of art and aesthetic experience, but it is sufficient to sketch the kind of scenario compatible with

such evidence. The archaeological record shows that the capacity for art and aesthetic experience, conceived in their broadest sense, has been part of our natural endowment probably since the dawn of our own genus. This capacity for expressing ideas through material culture was intimately associated with symbolic and abstract cognition and with cultural meaning. Early artistic activities were associated with the production of engravings, coloring with mineral pigments, and body ornaments. Such traditions appear to have been geographically and chronologically limited and distinct, making it unlikely that even the earliest manifestations shared a common meaning and were bound to a single social or individual function. It is especially unlikely that they played a similar role with our commonly held notion of art. Once this early capacity was in place, demographic and ecological conditions contributed to making true creative explosions possible, such as the one that happened at the Middle-Upper Paleolithic transition in Europe. They seem to have been related to increases in population size, where skilled individuals transmitted their knowledge to others and to enhanced altruism and cooperation, and were probably not related to additional specific cognitive innovations (Powell, Shenan, & Thomas, 2009). Population and ecological dynamics also explain why such creative explosions dwindled in time (Mellars, 2009).

Granting that our genus acquired early on the capacity for abstract expression of their symbolic cognition through material culture, can it be assumed that the necessary neural systems "appeared" around the same time? The neuroscientific evidence suggests that it cannot. Art and aesthetic experience are grounded on distributed nonspecific neural systems involved in many other domains of human life. Some of these could have appeared when our species emerged and were even crucial for its adaptive success. We share, however, many important aspects of neural systems that now constitute the foundations of aesthetic experience with some of our primate relatives, which suggests we inherited them from distant ancestors. Moreover, the fact that in humans these systems play important roles in other spheres of everyday life suggests that their evolution might have been subjected to multiple and diverse adaptive pressures with no direct relation to art and aesthetic experience.

In sum, artistic activities and aesthetic experiences, broadly conceived, seem to have evolved by integrating preexisting neural systems common to other primates with innovations that occurred throughout the human lineage. Such a process intertwined with the evolution of cognitive and affective processes linked to other human activities was the result of more than one selective pressure, probably involving more than one adaptive advantage. Once the necessary neural systems were in place, humans began expressing and experiencing symbolic meaning through many different forms of material culture. Such activities were intimately related to social and cultural practices. They were likely profoundly affected by group size, make-up (kin and nonkin living together in the same group), and social dynamics. The challenge for future research is to characterize the evolutionary modifications to the underlying neural systems with greater detail and to determine the way they coevolved with other cognitive faculties in relation to the interplay of mutually reinforcing or competing selective pressures.

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