CHAPTER 6

Constraining Hypotheses on the Evolution of Art and Aesthetic Appreciation*

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> If it were our purpose in this chapter to say what is actually known about the evolution of human cognition, we could stop at the end of this sentence. (R. C. Lewontin, 1990)

Researchers have attempted to explain the evolution of aesthetic appreciation and art for a long time. By the early twentiethth century, and even before the end of the nineteenth century, Darwinian-grounded reasoning had already led to some interesting conclusions. For instance, Clay (1908) argued that the pleasure we take in looking at or listening to beautiful things played an important adaptive role throughout the evolution of our species. According to him, this affective dimension of aesthetic appreciation grew out of the need to assess the suitability of environments. This viewpoint anticipated current models of the origins of aesthetic preference based on the emotional reactions to environments depending on their resources and potential dangers (Kaplan, 1992; Orians, 2001; Orians & Heerwagen, 1992; Smith, 2005). Other early work on "the primitive source of the appreciation of beauty" (Allen, 1880, p. 30), as well as its evolutionary history, was based on sexual selection, also a popular explanation in recent studies (Etcoff, 1999; Miller, 2001):

> Man in his earliest human condition, as he first evolved from the undifferen-
> tiated anthropoidal stage must have possessed certain vague elements of
> aesthetic feeling: but they can have been exerted or risen into conscious promi-
> nence only, it would seem, in the relation of primaeval courtship and wedlock.
> He must have been already endowed with a sense of beauty in form and
> symmetry (. . .). He must also have been sensible to the beauty of colour and
> lustre, rendered faintly conscious in the case of flowers, fruits, and feathers,
> but probably attaining its fullest measure only in the eyes, hair, teeth, lips,
> and glossy black complexion of his early mates (. . .). In short, the primitive
> human conception of beauty must, I believe, have been purely anthropinistic—
> must have gathered mainly around the personality of man or woman; and all
> its subsequent history must be that of an apanthropinisation (. . .), a gradual
> regression or concentric widening of aesthetic feeling around this fixed point
> which remains to the very last its natural centre. (Allen, 1880, pp. 450-451)

Richard Lewontin's (1990) skepticism regarding our knowledge about the evo-
lutionary history of cognitive processes stems from its largely speculative nature.
The views expressed by Allen (1880) and Clay (1908) on this topic, as well as the
later accounts (Etcoff, 1999; Kaplan, 1992; Miller, 2001; Orians, 2001; Orians &
Heerwagen, 1992; Smith, 2005), are susceptible to Lewontin's (1990) criticisms.
In paraphrasing this author, we must admit, first, that most hypotheses about the
evolution of art and aesthetic appreciation lack a solid grounding in facts, and,
for the most part, we have no means to assess their validity. Second, it is extremely
difficult to determine that aesthetic appreciation has actually been shaped by natural
selection, given that this involves demonstrating that survival probabilities differed
among individuals with different variants of this trait. Third, even if there actually
were differences in reproductive rates, the driving force of natural selection requires
individuals to differ genetically in relation to the particular trait, and there is no
certain proof of such differences for aesthetic appreciation. These and other points
led Lewontin to caution against taking plausible scenarios for demonstrated truth
about the evolution of cognition, and we believe the same can be said about art and
aesthetic appreciation.

Most of our knowledge about the evolution of our lineage relies on inferences
from fossil remains, material culture, and ancient DNA. However, there is little in the
fossil record—not to mention ancient DNA—that can be used to ground hypotheses
about the evolution of cognitive traits. Even the suitability of using material remains,
such as tools, signs of habitation, or burials, to infer mental capabilities is a matter
of much controversy. We believe that explanations of the evolution of aesthetic
appreciation should be firmly grounded on knowledge about the evolution of our
species, the cognitive processes involved underlying this mental faculty, as well
as the evolution of their neural correlates. In this chapter, we will review facts from
paleoanthropology and comparative neuroscience, which should be accounted for
by (and could serve as constraints on) hypotheses about the evolution of art and
aesthetic appreciation. In this attempt, we will focus most of our attention on the
possible evolution of the brain regions that have been implicated in aesthetic
preference by recent neuroimaging studies.

HUMAN EVOLUTION AND ARCHAEOLOGICAL EVIDENCE
OF AESTHETIC PRODUCTION

The basis for our classification of living beings was set by Linnaeus (1735). The highest place in this scheme was occupied by the order *Primata* (the first): humans and their closest relatives. The idea of evolution as an ascending scale is common among popular thinking, and it has permeated research in human evolution since its scientific beginnings. Until fairly recently, human paleontology favored a similar linear model. Human evolution was regarded as a straight line leading from our ancestors shared with apes to modern humans. Several stages were identified along this line, including the Australopithecine, Paranthropine, and Neanderthal phases (Brace, 1965). This sequential view found support in a seemingly ordered fossil record, with older specimens resembling current apes and recent ones exhibiting many more similarities to ourselves.

However, by the end of the 1970s new fossil evidence had made such a simple conception of human evolution untenable. The Kenyan Koobi Fora site yielded hominid remains that belonged to the same time interval but showed striking mor- phological differences. Some specimens were characterized by a robust appearance and a small cranium, while others were gracile and had slightly larger crania. The variation among these exemplars is such that they are currently included in three different species: *Paranthropus boisei*, *Homo habilis*, and *Homo ergaster*. This was the first sign of a previously unrecognized complexity and variety of human ancestry, but certainly not the last. In fact, recent findings in Central and Eastern Africa, as well as Southeast Asia, suggest that more than one hominid form has existed at each point in time almost since the very beginning of our family, and probably until only 20,000 or 30,000 years ago.

Most researchers would agree that fossil remains and molecular data indicate that hominids first appeared about 6 or 7 million years ago, somewhere in the African continent. The earliest specimens, from sites dated to between 5 and 7 million years ago have been attributed to three different species: *Sahelanthropus tchadensis*, *Orrorin tugenensis*, and *Ardipithecus ramidus*. Given the fragmentary state of these remains, and the difficulties inherent in their comparison, there is much discussion as to the validity of their hominid status. The earliest undisputed evidence of completely bipedal hominids is close to 4 million years old. This is the estimated age of some of the *Australopithecus anamensis* and *Australopithecus afarensis* specimens found in East Africa. Their most notable features include the presence of primitive traits, such as a small braincase, large canines, large molars, and certain remnants of arboreal specializations.

One of the most important events in human evolution was the splitting of the robust and gracile lineages between 3.5 and 2.5 million years ago. This divergence led to two distinct hominid adaptive strategies. One of the lineages became specialized in a diet consisting of hard vegetable materials and developed massive jaws, molars, and sagittal crests. The other lineage, the gracile one, turned to extrasomatic adaptations to survive. Undisputed evidence indicates *Homo habilis* was the first hominid to develop a stone-tool industry, known as Oldowan, the

earliest evidence of which dates to about 2.5 million years ago. When climate changes led to the disappearance of the robust lineage, close to 1 million years ago, it had spread across Africa and diverged into at least 3 distinct species (*Paranthropus boisei*, *Paranthropus aethiopicus*, *Paranthropus robustus*). Conversely, by 1.7 million years ago, the gracile lineage had arrived at Asia and developed a new, more sophisticated and varied lithic industry: Acheulean. Pleistocene hominids diverged into different species, including *Homo georgicus* in the Caucasus, *Homo erectus* in Asia, and *Homo ergaster* in Africa.

By 300,000 years ago, Neanderthals had settled in subglacial Europe and the Middle East. Meanwhile, in warmer East Africa, a new species was about to appear. The earliest exemplars of our species, *Homo sapiens*, are between 150,000 and 200,000 years old. This new species began sweeping across the old continents when temperatures rose, about 70,000 years ago. They arrived at Australia probably about 50,000 years ago, and moved into Europe before 30,000 years ago, displacing the Neanderthals, and crossed the Bering Strait into America between 30,000 and 15,000 years ago.

Each of these hominid species is characterized by a set of distinctive features, and they represent different adaptive alternatives. Although they share common ancestors, they cannot be placed along a single morphological or cognitive line leading from apes to humans. The branching of lineages within the hominid family probably led to different ways of solving adaptive problems, and for a long period of time hominids survived without manufacturing stone tools, let alone works of art.

There are different views on the origin of human behavioral modernity, which includes the capacity to create objects and depictions for aesthetic appreciation, as well as those endowed with a symbolic function. These approaches can be placed on a continuum between two contrary hypotheses. One of these, which we will refer to as the "revolution hypothesis," sees the archaeological record as pointing to a recent and rapid emergence of modern human behavior between 50,000 and 40,000 years ago. Some of the proponents of this perspective have argued that this sharp shift to the kinds of archaeological remains found in European Upper Paleolithic sites, such as intentional burials; ornamentation of tools, bodies and cave walls; elaboration of bone and ivory objects; novel blade technologies; as well as evidences of complex exchange relations, among others, are evidence of a substantial change in human cognition (Mellars, 1991) and its neural substrates (Klein, 1995). This rich archaeological record is seen to contrast with Middle Paleolithic remains, which are viewed as evidence of a simpler and less varied lithic technology, lower effectiveness of resource exploitation, and absence of symbolic behavior (Hensilwood & Marean, 2003).

Conversely, at the other end of the continuum, a number of reinterpretations of the archaeological record have recently questioned the place and time of the appearance of modern human cognition. They have shown that the revolution hypothesis ignores problems with the application of European-based prehistoric periodization systems to other regions; differences in the abundance and richness between European, African, and Asian archaeological sites; and population movements (Hensilwood & Marean, 2003). The alternative explanation, which we will refer to as the "gradualist

hypothesis," argues that, contrary to the predictions made by the revolution hypothesis, the set of behaviors taken to indicate human cognitive modernity did not appear at the same time and place. McBrearty and Brooks (2000) have presented abundant evidence supporting the notion that the Upper Paleolithic remains found in Europe are the result of a gradual and continuous accumulation of novel behaviors during a long period of time. In fact, as work progresses in African archaeological sites, it is becoming increasingly clear that such activities as the use of ochre, engraving, bone working, as well as complex subsistence strategies, appeared much earlier than posited by the revolution hypothesis (d'Errico et al., 2003; Hensilwood, d'Errico, Marean, Milo, & Yates, 2001). For instance, ornamental sea shells, eggshells, and perforated bones have been found in some African sites dated to 100,000 years. Decorative stones have appeared in 130,000-year-old Nigerian sites. The use of ochre has been documented in a number of sites spanning the last 300,000 years (McBrearty & Brooks, 2000). However, early evidence of aesthetic appreciation is not restricted to the African continent. A gradual, though later, transition to fully modern behaviors is also apparent in the South Asian archaeological record (James & Petraglia, 2005). The recent accumulation of new data, together with the reinterpretation of earlier evidence, seems to confirm Martin's (1998) observation that the mosaic nature of evolution makes the origin of human uniqueness at a particular point in time a very unlikely scenario.

Hence, recent revisions of the archaeological record from a global, not just European, perspective suggest that the origin of art, symbols, and aesthetic appreciation is diffuse, extended in space, and continuous in time, with deep roots in our Middle Paleolithic ancestors' cognitive and neural structures. The evidence for this origin appears throughout a long period of time, initially scarcely, but later growing in abundance and variety. Only by neglecting the African and Asian archaeological record is it possible to be surprised at the "sudden" artistic explosion of the European Aurignacian. This set of cultural manifestations had been gradually growing since the appearance of our own species and left some early samples, not in Europe, but in Africa. The murals found in caves in Southern France and Northern Spain are sophisticated and beautiful manifestations of cognitive processes that were probably present at the dawn of our own species, some of which might have been inherited from earlier ancestors. Rather than signs of a cognitive modification (or neural or genetic, for that matter), they seem to be the result of a long process of cultural evolution that gradually led to increasingly sophisticated and varied expressions of an underlying modern creative capability and aesthetic preference, which are, possibly, as old as our species.

EVOLUTION OF THE NEURAL BASES OF AESTHETIC PREFERENCE

To consider language, moral reasoning, or aesthetic appreciation as single and unitary cognitive processes may suggest that each of these cognitive faculties owes to a single, separate piece of computing machinery. However, viewing cognitive mechanisms as the result of the modification and novel combination of previously

existing subcomponents has proved very fruitful in beginning to understand their structure and evolution (Marcus, 2004). Evolutionary approaches to human behavior and cognition must not lose sight of the fact that such human behaviors as admiring the beauty of a sculpture or creating an artwork are the result of the interplay of different cognitive processes, probably none of which are exclusive to the task. This has been highlighted by recent models of aesthetic experience (Chatterjee, 2003; Leder, Belke, Oeberst, & Augustin, 2004). Most contributions to the study of the evolution of aesthetic appreciation implicitly or explicitly assume that this cognitive trait appeared at some stage in human evolution, most commonly during the Pleistocene (Orians & Heerwagen, 1992). However, this assumption needs to be justified, given that it is not inconceivable that humans share some of the cognitive and neural underpinnings of aesthetic appreciation with other primates, and thus, may predate humans themselves. This, which might intuitively seem far-fetched, has recently been demonstrated for language. Some of the cognitive processes involved in language comprehension and acquisition, and hence, presumed to be specifically human traits, have been identified in monkeys (for reviews of this research, see Tincoff & Hauser, 2005; Weiss & Newport, 2006). Similarly, Flack and de Waal's (2000) division of human morality into four building blocks allowed them to identify its possible evolutionary roots in our primate relatives. This suggests that not all the constituent cognitive operations subservient to human morality and language appeared after the human and chimpanzee lineages diverged. In fact, it suggests that they appeared long before humans, and that human language and morality evolved, in part at least, by using preexisting building blocks. In this section, we will explore the question of whether brain regions involved in aesthetic preference show any kind of special feature in humans, or whether they seem to have changed little since our lineage separated from our closest living relatives. It is very possible that not all the neural structures involved in aesthetic preference (and the functions they perform), have undergone the same degree of transformation since the appearance of the human lineage. We believe that differences and similarities between human and nonhuman primates in the brain regions shown to be involved in aesthetic preference by neuroimaging studies, can offer clues to researchers approaching these cognitive processes from an evolutionary perspective.

A caveat before we proceed: As Sejnowski and Churchland (1989) pointed out, the brain can be organized in several hierarchical levels. These include systems, maps, networks, individual neurons, synapses, and molecules. As with any other cognitive operation, there is no way of determining which level of analysis is the most relevant to the study of the neural correlates of aesthetic preference. Additionally, the evolutionary emergence of such a capacity may owe to alterations in any set of these levels. In this case, though, information about the neural underpinnings of this cognitive operation is limited to one of these levels (systems), and the little knowledge we have about how the human brain evolved prevents reasonable hypotheses about modifications at most of the other levels. Hence, our analysis will be restricted to the higher levels in the organizational hierarchy of the brain.

Cognitive Operations Involved in Aesthetic Preference

In order to address the question previously outlined, we first need to determine the building blocks of aesthetic appreciation. The models elaborated by Chatterjee (2003) and Leder and colleagues (2004) provide reasonable guidelines to carve aesthetic appreciation into basic components. Although Chatterjee's (2003) proposal is a model of aesthetic preference for a broad range of visual objects grounded on visual neuroscience, and Leder and colleagues' (2004) an information-processing model of aesthetic judgment of artworks, they represent complementary views of cognitive and affective operations involved in aesthetic appreciation (Vartanian & Nadal, in press). Given that our main concern here is the relation between brain and aesthetic appreciation, Chatterjee's (2003) framework is better suited to our purposes. Chatterjee suggested that aesthetic preference involves three processing stages, common to the perception of any visual stimulus. During early visual processes, simple components are extracted and analyzed in different brain areas. Operations in the intermediate stage segregate some elements and group others, forming coherent representations. In late stages, certain regions of the object are selected for further scrutiny, memories are activated, objects are recognized and associated with meanings. In the case of visual stimuli found to be aesthetically pleasing or displeasing, these operations elicit emotional processes, which feed back into the system of via attentional mechanisms. There is a second output, resulting from decision-making processes. Chatterjee (2003) suggested that the involvement of visual brain regions in processing aesthetic stimuli is the same as in the processing of any other kind of visual stimuli. What sets aesthetic preference apart from other cognitive processes involving visual stimuli is precisely the engagement of additional nonperceptual processes, such as emotions and decision making.

Recent neuroimaging studies have revealed a basic picture of the neural correlates of these cognitive and affective processes. Affective processes involved in aesthetic appreciation seem to be mediated by the orbitofrontal cortex (Kawabata & Zeki, 2004), caudate nucleus, anterior cingulate cortex, as well as the strengthening of early visual processes in the occipital cortex (Vartanian & Goel, 2004). Recognition and meaning attribution in aesthetic appreciation seem to be related with activity in the temporal pole (Jacobsen, Schubotz, Höfel, & von Cramon, 2005), and decisions seem to be mediated by the lateral prefrontal cortex and the frontal pole (Cela-Conde et al., 2004; Jacobsen et al., 2005). If indeed these are the main brain regions that support aesthetic preference, it follows that knowledge about their evolution is basic to understand the evolution of aesthetic preference itself.

A comprehensive understanding of the evolution of the human brain, as well as of certain specific regions, requires taking into account general principles of brain evolution that operate across a broad range of animals, accounting for current brain features that seem to be specifically human, and tracing these features in the fossil record. Space limitations will allow us only to briefly outline some of the main ideas and to require us to restrict ourselves to our regions identified by neuroimaging studies of aesthetic preference, which were noted above. Readers who wish to delve deeper in research on human brain evolution will find Rilling (2006) and

Schoenemann (2006) good critical reviews of current knowledge both clarifying and interesting.

Evolution of the Human Brain

After the human lineage split from the lineage leading to chimpanzees, there was no appreciable increase in brain size. The cranial capacity of early australopithecines, such as *Australopithecus afarensis*, is close to 400 cc, almost identical to that of current chimpanzees. In relation to body size, cranial capacity did not vary much within the robust lineage. However, an extra-allometric increase in brain size accompanied the appearance of the first specimens of our own genus, *Homo habilis*. This means that although there is no evidence of increased body weight in comparison with other species, the cranial capacity of *Homo habilis* is estimated at 700 to 750 cc. There is a general agreement that this represents a notable increase and is somehow related with the appearance of lithic cultures. The cranium of *Homo erectus*, reaching 900 to 1,000 cc, was larger than that of *Homo habilis*, though so was its body. Hence, this increase in brain size seems to owe to a general increase in body size (Hublin, 2005). Conversely, brain growth in later hominids, such as Neanderthals or modern humans, seems to have been extra-allometric, given that the sizes of their bodies did not vary much; but the average cranial capacity in our species is about 1,350 cc.

Comparative studies suggest that the subcortical components of the brain have not undergone a dramatic change in size or organization during human evolution. This means that the primary source of increase in cranial capacity observed in the human fossil record is related to increases in the cerebral cortex. Moreover, there is evidence suggesting that in fact most of the cortical expansion that occurred after the human lineage split from that of chimpanzees is due to the enlargement of the neocortex (Changeux, 2005; Zilles, 2005). However, it appears that not all functional regions of the neocortex have undergone the same increase in size. Whereas primary sensory and motor regions seem to have grown little, or even occupy a smaller relative area than in other primates, there seems to have been an extraordinary increase of the multimodal association cortex during human evolution (Changeux, 2005; Zilles, 2005). This conservation is also apparent at finer levels of analysis. The study of cytoarchitectonic and neurochemical properties of motor and somatosensory cortices of macaques and humans carried out by Zilles and colleagues (1995) revealed great similarities between both species, suggesting that brain regions involved in the processing of somatosensory and motor information are largely conserved in these species. Thus, our review of the findings on the evolution of human brain areas involved in aesthetic preference will focus on multimodal association cortical regions.

The Visual System

Vartanian and Goel's (2004) neuroimaging study of aesthetic preference for paintings revealed that activity in occipital visual regions was greater when participants gave a higher preference rating to the stimulus they were seeing than when

they gave a lower score. Previous studies suggest that preferred stimuli engage attentional mechanisms (Kaestner & Ungerleider, 2000; Poghosyan, Shibata, & Ioannides, 2005) or affective processes (Lang et al., 1998) that enhance their processing at early visual stages.

Although the region occupied by the primary visual cortex in humans is 1.5 times larger than it is in chimpanzees, in relative terms it is almost half the size expected for a primate brain of 1,350 cc. It seems, thus, that throughout the course of human evolution, occipital regions that carry out the initial processing of visual information have expanded less than the overall brain. But whereas size variations are relatively easy to measure, the comparative study of the organization of the visual cortical system in monkeys and humans is hampered by the lack of broad consensus regarding their partition into discrete areas. Several reviews on homologies between monkeys and humans in the cytoarchitecture and function of the visual cortex note that the only undisputed homologies refer to areas V1, V2, V3, and MT/V5 (Orban, Van Essen, & Vanduffel, 2004; Sereno & Tootell, 2005; Van Essen, 2005). As Orban and colleagues (2004) note, the retinotopic organization and functions of brain areas involved in early visual processing—V1 and V2—are largely conserved in humans. However, there are indications of certain derived aspects in area V1 of the human brain. Specifically, Preuss and Coleman (2002) reported evidence showing that humans differ from other primates in certain features related to the cortical representation of the magnocellular visual pathway. The data suggest some of these modifications appeared in the common ancestors of African apes and humans, whereas others appeared along the human lineage. Given that the magnocellular system is related to the processing of luminance contrasts, and that the perception of motion is impaired in isoluminant conditions, this system appears to be essential in analyzing motion. Other features that are associated with processing along the magnocellular stream include perspective, relative size of objects, and depth perception.

Whereas early visual areas tend to be homologous in humans and monkeys, as we move up the visual system hierarchy, homologies become less clear. For instance, area V3 supports virtually identical representations of the visual field in humans and macaques. However, Orban and colleagues (2004) noted that human area V3A is sensitive to motion cues and uses them to extract three-dimensional information, whereas the monkey area V3A does not share this function. Similarly, it seems that even though the posterior region of MT/V5 is conserved in humans, the homologues of the anterior part still remain unclear. It is not easy to determine the monkey homologue of human area V4 because its ventral and dorsal regions have evolved in different ways among primate species. Further downstream, additional differences have been identified. Studies reported by Orban and colleagues (2004) using comparative functional magnetic resonance imaging (fMRI) data and computerized brain warping suggest that the ventral and dorsal visual streams have not evolved in the same fashion along the human lineage. Specifically, the areas included in the ventral stream, related to object representation and categorization, have undergone a smaller expansion than those parts of the dorsal stream involved in the representation of space and the analysis of visual information to organize action (Orban et al.,

2004). Barton (2006) noted that the fact that the parietal areas of the dorsal stream receive only information from the magnocellular system adds to the aforementioned idea of an enhancement of the magnocellular cortical representations during human evolution. The relative conservation of the ventral stream in humans is further evidenced by studies showing activity in human and monkey homologue brain areas during the perception of symmetry (Sasaki, Vanduffel, Knutsen, Tyler, & Tootell, 2005), representation (Munakata, Santos, Spelke, Hauser, & O'Reilly, 2001), and categorization of visual objects (Sigala, Gabbiani, & Logothetis, 2002).

Temporal Poles

The neuroimaging study of aesthetic judgment carried out by Jacobsen et al., (2005) revealed that rating the beauty of visual geometric stimuli was associated with a greater activity in the left temporal pole, compared with when participants rated the symmetry of the stimuli. Backed by the results from previous work, the authors suggested that this region could be involved in the creation of a broad affective and semantic context based on past experiences in which to frame decisions about beauty of visual stimuli.

Rilling and Seligman (2002) compared several aspects of the temporal lobe across a broad sample of primates, including humans. Their results revealed that during human evolution, the temporal lobe grew in surface and volume, as well as in white matter, resulting in a larger-than-expected proportion of the brain. However, there is evidence suggesting that the temporal lobe of humans is not merely an allometricaly enlarged ape temporal lobe. The amount of white matter in the human temporal lobe is greater than predicted by primate allometric trends, suggesting that temporal-lobe connectivity patterns have undergone a certain amount of reorganization since the appearance of the human lineage, which is consistent with Schenker, Desgouttes, and Semendeferi's (2005) results. Rilling (2006; Rilling & Seligman, 2002) suggested that this reorganization might be related to the appearance and expansion of language-related areas in the temporal lobe of humans, especially in the left hemisphere. They based this hypothesis on studies that have shown that language areas occupy a large portion of the human lateral temporal lobe, including the temporal pole. In monkeys, this region appears to be mostly involved in object recognition. Thus, it seems that in humans, the visual-object processing stream has shifted ventrally to allow for the expansion of language and speech-related areas on the lateral surface.

Despite this difference in the functional involvement of lateral and ventral regions of the human and nonhuman primate temporal lobes, it seems that most of the functions of the temporal pole are homologous. Recent studies carried out with monkeys suggest that regions in the left temporal lobe of humans, including the temporal pole, which have been involved in the processing of speech, might have a long evolutionary history of processing information relative to vocal communication. Poremba, Malloy, Saunders, Carson, Herscovitch, and Mishkin (2004) found that the right and left temporal poles of macaques are specialized in the processing of acoustic stimuli. But whereas activity in the right hemisphere was

associated with a broad spectrum of sounds, including nonvocal sounds, ambient background noise, and human speech, activity in the left dorsal temporal pole was greater than in the right hemisphere for species-specific monkey vocalizations. The authors believe this could represent a precursor of auditory language processing in the human brain. Belin's (2006) review of the comparative processing of vocal information also emphasizes this coincidence of lateralized function in human and nonhuman primates.

But there seems to be additional functional homologies. The human temporal pole has been related to the use of past experiences to generate a broad semantic and emotional context in which to interpret the information being processed. Kondo, Saleem, and Price (2003) showed that the temporal pole of monkeys is strongly connected with orbital and medial prefrontal networks, suggesting its involvement in the integration of emotional, mnemonic, and sensory processes. This functional homology converges with the results reported by Croxson and colleagues (2005), showing that the connectivity patterns of the temporal and prefrontal cortex of humans and macaques are very similar.

Finally, the temporal pole seems to play a central role in object recognition in humans. Lesions to this region impair the ability to recognize and recall specific entities, especially familiar objects and faces (Nakamura & Kubota, 1996). This function also finds a homologue in the monkey. It has been shown that neurons in the anterior temporal cortex are involved in the higher-order processing of object-related visual information and can become sensitive to the presentation of exemplars of a trained category (Vogels, 1999). Likewise, other studies, reviewed by Nakamura and Kubota (1996), suggest lesions to the monkey temporal pole produce deficits in the recognition of the experimenters' gloves, food, or live snakes, but not in the discrimination of unfamiliar objects or patterns.

Frontal Lobes: General Features

Terrence Deacon (1997) argued that the human prefrontal cortex is about twice the expected size for a hominoid brain the size of ours. This increase has often been associated with humans' unique cognitive traits, such as language or symbolic representation; but Ralph Holloway's (1996) results indicated that the volume of this region lay within predicted values, casting doubts on the relation between the size of the prefrontal cortex and human cognitive faculties. In order to reach an empirical clarification of this matter, Semendeferi and Damasio (2000) used structural magnetic resonance to measure the sizes of different brain regions of modern humans, chimpanzees, gorillas, orangutans, and gibbons. Images were reconstructed to produce three-dimensional renderings of the cerebral hemispheres, which allowed the authors to calculate total hemispheric volumes, as well as the volumes of the frontal, occipital, and the combination of temporal and parietal lobes. Their results revealed a great homogeneity in the relative volumes of those sectors. Thus, their results provided no evidence of an increase in size in any part of the prefrontal cortex during human evolution (Semendeferi & Damasio, 2000).

It might be the case that variation in sheer size is not the key to understanding the evolution of neural correlates of cognitive processes. It is known that increases in primate brain size involve an expansion of cortical area rather than thickness. And given that this surface expansion does not involve an equal increase in cranial size, the cortex must increase the degree of folding. Zilles, Armstrong, Schleicher, and Kretschmann (1988) compared the pattern of rostro-caudal gyrification indices—the extent to which the cortex is folded, forming sulci and convolutions—of human and nonhuman primate brains. They found that the human pattern, which revealed maximum gyrification indices for the prefrontal, posterior temporal, and anterior parietal cortex, was strikingly different from that of prosimians and monkeys. When compared with brains of chimpanzees, gorillas, and orangutans, the human brain does not appear that special, except for one fact: the unusually high gyrification index of the prefrontal cortex.

With techniques that afforded greater precision, Rilling and Insel (1999) continued the research on the gyrification of primate brains. They used structural magnetic resonance to measure the brains of 44 specimens belonging to 11 different primate species. Their results confirmed that, overall, larger brains have greater gyrification indices. However, there are two regions in the human brain that exceed the expected value: the prefrontal cortex and the posterior temporal-parietal cortex. The authors suggested that the increase in gyrification of these regions during human evolution could constitute part of the neural bases that led to the appearance of some of our unique cognitive faculties.

Increases in the surface of prefrontal and parietal cortices necessarily lead to an increase in intracortical connectivity if function is to be maintained. This, in turn, would require increasing the proportion of white matter in these areas. Schoenemann and colleagues (2006) searched for evidence of this increase in white matter in the human prefrontal cortex. They measured grey matter, white matter, and volumes of the prefrontal cortex, as well as the total cortex, of male and female individuals belonging to 11 different primate species. Results revealed that the correlation between the percentage of prefrontal white and grey matter was very weak. This suggests that connectivity might vary throughout evolution with relative independence from variations in neural numbers. Furthermore, there were significant differences in the proportion of white matter in the prefrontal area between human and nonhuman primates, whereas there were no such differences with regard to grey matter (Schoenemann, 2006). Taken together, these results suggest that white matter in the prefrontal cortex—either through increase in number of glial cells, reorganization of connectivity patterns, or both—might have played a crucial role in the development of sophisticated cognitive processes supporting a variety of characteristically human traits. However, Sherwood, Holloway, Semendeferi, and Hof (2005) criticized the proxy for prefrontal cortex used in this study, as well as the composition of the sample included, and suggested that the increase in prefrontal white matter is much smaller than suggested by Schoenemann and colleagues' (2005) results. In fact, it is difficult to ascertain whether this overabundance of prefrontal white matter represents an extra-allometric increase, or whether, as argued by Sherwood et al. (2006), it is associated with elevated energetic costs

derived from maintaining longer axonal projections and larger dendritic arbors in such a large brain as ours. In any case, given the evidence presented by Bush and Allman (2004), which showed that primates have a greater amount of grey matter in the frontal cortex relative to the rest of the cortex than carnivore mammals, it seems that the increase in prefrontal white matter throughout human evolution represents the extension of a general primate trend.

Orbitofrontal Cortex

Activity in the orbitofrontal cortex was identified by Kawabata and Zeki (2004) while participants decided about the beauty of diverse artistic visual stimuli. The fact that many studies have observed activity in this region in association with primary (Francis et al., 1999; O'Doherty, Deichmann, Critchley, & Dolan, 2002) and abstract (O'Doherty, Kringelbach, Rolls, Harnak, & Andrews, 2001) rewarding stimuli, suggests that its role in aesthetic preference might be to represent the reward value of each visual stimulus.

The comparison of the orbitofrontal cortex of a large number of macaques and humans revealed that their sulcal patterns were very much alike (Chiavaras & Petrides, 2000), though the human pattern was more variable and showed a greater degree of intricacy. In both species, there are four main sulci in each hemisphere. These form five main gyri: a medially positioned gyrus rectus, parallel to which runs the medial orbital gyrus. Between the latter and the lateral orbital gyrus lay the anterior orbital gyrus and the posterior orbital gyrus. Thus, there seems to be a high degree of conservation regarding the sulcal pattern of the human orbitofrontal cortex.

Semendeferi and colleagues' (1998) comparative analysis of Brodmann's area 13, located in the posterior orbitofrontal cortex included a quantitative study of the microstructural organization of this area and estimated its volume for humans, chimpanzees, bonobos, gorillas, orangutans, and gibbons, as well as rhesus monkeys. Although they included relatively small samples, some of their results might turn out to be relevant to the study of the evolution of aesthetic appreciation. Despite overall similarities, which led Semendeferi, Armstrong, Schleicher, Zilles, and Van Hoesen (1998) to consider the state of area 13 in humans as primitive, meaning conservative, there are several features that distinguish humans from other sampled apes. For instance, area 13 in humans and bonobos is relatively smaller than in other apes, which, together with other features, suggests an increased number of orbitofrontal cortex cytoarchitectonic regions. The cell density of this area in humans was the lowest of all hominoids, and together with gibbons, they showed the lowest grey-level indices, meaning that there is greater space filled by axons and dendrites.

This picture of a mosaic of primitive and derived aspects of the organization of the human orbitofrontal cortex was also the result of Van Essen's (2005) comparison with macaques. The overall layout of the cortical areas is much the same in both species, as is their neighboring relations. As for relative sizes, lateral orbitofrontal areas seem to be the most conserved. Although there are some differences between the medial and posterior areas of both species, it is the anterior region, occupied by

area 10, which shows the largest amount of differences. Whereas in humans this area occupies 4.5% of the cortex and is constituted by five subdivisions, in macaques it represents 1.4% of the cortex and shows two subdivisions (Van Essen, 2005), confirming Semendeferi and colleagues' (1998) aforementioned prediction.

Rolls' (2004) review of the functions of the primate orbitofrontal cortex suggests that this region is functionally conserved in humans in that, as in monkeys, it includes representations of smell, taste, food texture, ventral-stream visual information, as well as facial information. These representations are used to identify the stimuli being processed and to establish their reward value. Moreover, the orbitofrontal cortex of monkeys and humans seems to be a crucial element in learning stimulus-reward associations and correcting them when contingencies are altered.

Anterior Frontal Cortex

As previously mentioned, Jacobsen and colleagues (2005) recorded activity in the frontal pole while participants performed aesthetic judgments of geometric visual stimuli. In light of previous studies (e.g., Zysset, Huber, Ferstl, & von Cramon, 2002), it seems that this brain region plays a fundamental role in a broad spectrum of evaluative judgments. Petrides and Pandya (1999) compared the neural organization of Brodmann's area 10, the designation of the cytoarchitectonic region occupying the frontal pole, in macaques and humans. Their results revealed that the architectural features that distinguish this area from the neighboring ones are largely the same in both species. This suggests that there has been little change in the types and distribution of neurons across cortical layers in this brain area throughout human evolution.

Semendeferi, Armstrong, Schleicher, Zilles, and Van Hoesen (2001) carried out a quantitative and qualitative analysis of Brodmann's area 10. They compared data from macaque, gibbon, orangutan, gorilla, chimpanzee, bonobo, and human brains. Although their results are preliminary, due to relatively small sample sizes, they reveal some interesting commonalities and differences among hominoids. For instance, the study showed that area 10 is found in the frontal pole in humans as well as Asian and African apes, except for gorillas, which exhibit a rather particular organization of this area. On the other hand, there are certain features that set humans apart from other hominoids with regard to this specific brain region. First, it is larger, both in relative and absolute terms, than that of other apes. However, when the data are transformed into logarithmic scales and regressed for all hominoids, the observed value for the size of area 10 in humans is just above the expected value. Holloway (2002) calculated this increase to represent approximately 6%. Second, although in humans the absolute number of neurons is larger, the neural density is the lowest among hominoids, allowing greater space for connections within the same and other areas. Specifically, Semendeferi and colleagues (2001) noted that "Humans seem to have more space available for connections in layers II and III, which may indicate increased communication between area 10 and other higher-order association areas in our species" (Semendeferi et al., 2001, p. 238).

Lateral Prefrontal Cortex

The studies carried out by Cela-Conde and colleagues (2004) and Jacobsen and colleagues (2005) revealed that rating the beauty of visual artworks and geometric designs engages the lateral prefrontal cortex. The hypothesis that this activity might be related to decision-making processes involving beauty of the visual stimuli presented in the studies is supported by previous studies (Heekeren, Marrett, Bandettini, & Ungerleider, 2004; Krawczyk, 2002).

Van Essen's (2005) review of the compared cortical organization of monkeys and humans revealed that the expansion of the prefrontal cortex was uneven during hominid evolution, suggesting that the lateral areas are the ones that have expanded the most. Despite this difference in the relative expansion of cortical areas, there seems to be a great similarity between humans and other primates regarding the neural architecture and functions of the lateral prefrontal cortex. Petrides and Pandya (1999) carried out a comparison of the cytoarchitecture and connection patterns of the human and macaque dorsolateral prefrontal cortex, which encompasses Brodmann's areas 8, 9, and 46. Results showed that there are no novel cytoarchitectonic areas in the human brain. In fact, they all exhibited similar characteristics in humans and macaques, such that the same architectonic features can be used to identify these areas in both species. This architecture is homologous to the extent that even the same subdivisions of the areas, namely 8Av, 8Ad, 8B, 9/46d, and 9/46v, were to be found in both species. A similar picture emerged after the comparative analysis of the ventrolateral prefrontal cortex of humans and macaques (Petrides & Pandya, 2001), which includes Brodmann areas 47/12 and 45. The cytoarchitectural criteria used to distinguish these two areas in monkeys and humans were largely the same as those used to differentiate both of them from the areas in the dorsolateral cortex. Again, even the finer-grained subdivisions of area 45 (45A and 45B) were distinguishable in both species.

At a functional level, similarities between monkeys and humans regarding the lateral prefrontal cortex have also been documented. Petrides (2005) noted that the lateral cortex of both monkeys and humans is functionally organized along a caudal-rostral axis. Lesion studies have shown that the caudal region of the prefrontal cortex (area 8) in monkeys contributes to the flexible switching of attention between stimuli and the selection of competing responses according to learned conditional rules. At the rostral end of the axis, the mid-lateral prefrontal cortex is involved in more abstract processes of cognitive control. Here, there is a further functional organization along a dorsal-ventral axis. Lesions to the mid-dorsolateral (areas 46 and 9/46) region result in impaired performance of working memory tasks that require monitoring the selection of stimuli or the occurrence of expected events. Lesions to the mid-ventrolateral prefrontal cortex (areas 47/12 and 45) affect the performance of executive functions, including the selection and comparison of stimuli stored in short- and long-term memory, as well as the performance of judgments based on them. Petrides (2005) reviewed several neuroimaging studies carried out with human participants to clarify the organization of lateral prefrontal areas, the results of which converge with the lesion studies carried out on monkeys.

Thus, the functions performed by the lateral cortex in humans—selection, monitoring and judgment—are also structured along both a caudal-rostral and a dorsal-ventral axis. Taking into account the aforementioned results obtained from monkey-lesion studies, it would seem that the functional organization of the human lateral cortex is a primitive trait. There are, however, certain differences. For instance, it is obvious that the recruitment of these functions for particular human cognitive abilities, such as language or even aesthetic appreciation, is absent in other primate species. Second, the kinds of information upon which these functions are carried out also seem to differ. Denys and colleagues (2004) used fMRI with human and nonhuman primate participants to show that the activation of the prefrontal cortex was much stronger in monkeys than humans when presented with visual objects. The authors interpreted this finding as the result of the multi-sensory nature of information reaching the human cortex, in contrast with the primarily visual information received by the monkey prefrontal cortex. Alternatively, it could also be due to the selective gating of visual information reaching the human prefrontal cortex (Denys et al., 2004).

Anterior Cingulate Cortex

The studies carried out by Vartanian and Goel (2004) and Jacobsen and colleagues (2005) recorded activity in this region while participants performed aesthetic preference tasks. Evidence from prior studies (Hornak et al., 2003; Lane, Reiman, Axelrod, Yun, Holmes, & Schwartz, 1998) suggests that its involvement in aesthetic preference might be related to the conscious awareness of emotions elicited by aesthetically pleasing visual stimuli. Although the anterior cingulate cortex is cytologically distinguishable from the posterior cingulate cortex in both monkeys and humans, there are also significant differences between both species. The most obvious one is the presence of two new areas in humans: 33 and 32. Moreover, the results obtained by Nimchinsky, Gilissen, Allman, Perl, Erwin, and Hof (1999) suggest that the anterior cingulate cortex of great apes and humans is characterized by a unique kind of neurons. These neurons, called spindle cells, and found in layer Vb, have not been found in other mammals, including other primate species. In humans, these cells represent 5.6% of pyramidal cells in traverse sections of this layer, and are found in clusters of 3 to 6 neurons. Among other hominoids, bonobos revealed the closest trend to humans, with spindle neurons, which in their case represent 4.8% of pyramidal cells, also clustering in packs of between 3 and 6. Conversely, no clusters were observed in common chimpanzees, gorillas, or orangutans, and relative abundance was 3.8%, 2.3%, and 0.6%, respectively. None were observed in gibbon samples. These results suggest that new kinds of neurons restricted to the anterior cingulate cortex appeared during the evolution of hominoids. These neurons became relatively more numerous along the lineage leading to humans and began to cluster together. Allman, Hakeem, and Watson (2002) noted that the greatest concentration of spindle cells in the human anterior cingulate cortex is found in its ventral region, the activity of which has often been recorded during the performance of emotional tasks (see Bush, Luu, & Posner, 2000

for a review). Nimchinsky and colleagues (1999) hypothesized that the main function of these neurons is to integrate affective information and transmit it to motor regions related to vocalization, facial expression, or autonomic functions. Allman and colleagues (2002) suggested that increased proportion of spindle cells could be related to the enhancement of emotional stability and self-control, and that, together with an enlarged anterior frontal cortex, it was a key factor in coping with the economic needs of human extended families.

Summary

Studies such as those highlighted in this section can constitute a starting point for hypotheses about the evolution of aesthetic preference, because they provide an initial sketch of the modifications that the neural underpinnings of this cognitive faculty have undergone during human evolution. Our review has revealed that some areas shown by neuroimaging studies to be involved in aesthetic preference are relatively conserved in humans, while others exhibit a number of derived features.

The orbitofrontal cortex presumably supports the representation of reward value of visual stimuli during aesthetic-judgment tasks. It seems that to a large extent, its sulcal pattern, cytoarchitecture, and functions are conserved in the human brain. The only derived features appear to be an enlargement of area 10 and a reduction in neural density. A similar picture emerges after reviewing the comparative literature on the frontal pole, involved in the decision-making stage of aesthetic preference: relative enlargement and reduction of the density of neurons. There is also a great cytoarchitectonic similarity between humans and monkeys in the other regions shown to be involved in decisions about the beauty of visual stimuli, the mid-dorsolateral and mid-ventrolateral cortex. In addition to a considerable enlargement during the evolution of our species, the main difference between both species is that in humans, these lateral regions seem to receive multisensory information, rather than mainly visual. Overall, the complexity of prefrontal-cortex connectivity patterns seems to have increased after our lineage split from chimpanzees some seven million years ago.

Activity within the temporal pole has been related to the creation of a mnemonic and emotional context for aesthetic preference. Our review has revealed that this region performs very similar functions in monkeys and humans, essential for the categorization and recognition of familiar objects, and the integration of emotion, memory, and sensory information. Even if temporal regions involved in language have expanded in humans, pushing areas of the object-centered visual stream further ventrally, they seem to bear a close phylogenetic relation to those underlying the processing of species-specific calls in monkeys.

Occipital visual areas, whose activity during aesthetic preference has been interpreted as the correlate of emotional or attentional engagement, show a mosaic of novel and primitive features. Whereas areas supporting early visual processing seem to be largely conserved, those involved in later stages seem to have changed somewhat. Specifically, the processing of spatial information and the organization of

visual information to guide movement seems to have been emphasized during human evolution, rather than object-centered visual analyses.

Finally, our review of comparative work on the anterior cingulate cortex, which probably plays a role in the conscious awareness of the affective state during aesthetic preference, has revealed two major modifications in cytoarchitecture: the appearance of two novel cytoarchitectonic brain areas, and the clustering of a kind of neuron unique to great apes and humans.

THE PRODUCT OF GENES AND CULTURE

The fact that structural and cytoarchitectonic modifications of the brain that occurred throughout the human lineage owe, ultimately, to changes in the developmental course of neural tissue has sometimes been overlooked by studies of brain evolution (Martin, 1998). Although these developmental processes are guided by genes, the relation between brain features and genes is, at present, far from straightforward. It is now known, for instance, that the expression of a certain gene may depend on the tissue, the developmental stage, as well as the context provided by other active genes. Furthermore, it seems that genes are largely pleiotropic, meaning that they are related to several aspects of brain development and function. Changeux (2005) hypothesized that the expansion of human frontal brain regions, as well as others, might be the outcome of an extended influence of (probably few) developmental genes. This hypothesis is backed by results showing striking differences in the regulation of gene expression in the cerebral cortex of humans when compared with other primates (Cáceres et al., 2003). Results by Oldham, Horvath, and Geschwind (2006) revealed that these differences are not common to all brain regions, and suggest that expression patterns might be especially derived in the association cortex, while relatively conserved in the primary visual cortex. Uddin and colleagues (2004) cautioned, however, that changes in gene-expression regulation in the brain are not restricted to the human lineage, but that they have also occurred in chimpanzees, as well as other ape and primate species.

Enard and colleagues (2002) studied the expression levels of mRNA and the expression patterns of proteins in samples from human, orangutan, chimpanzee, and macaque tissues. Their results showed that there are more gene-expression differences between humans and other species in the brain than in other organs. This finding suggests that changes to gene-expression levels in the brain have been especially marked during human evolution. Similar results were reached by Dorus and colleagues (2004), who analyzed the evolution rate of proteins related to genes underlying biological functions of the nervous system in several species of primates and rodents. They found that primates showed a higher evolution rate than rodents, especially for genes involved in the development of the nervous system. This trend was not as prominent for genes related to routine physiological processes. Moreover, their results also revealed that, within the primate order, these genes had undergone an especially rapid evolution along the human lineage, a finding they related to the increased size and complexity of the human brain. Pollard and colleagues (2006) identified a series of chromosomal regions that are typically conserved in mammals

but seem to have suffered a highly accelerated evolution throughout the human lineage. Their results reveal that many of these chromosomal regions house genes that carry out regulatory and neurodevelopmental functions. Rates of change in amino-acid sequences that are faster than expected under a neutral model are usually taken as a sign of positive selection and of increased evolutionary success (Amadio & Walsh, 2006). Hence, modifications to developmental processes in the brain seem to have been guided by strong positive selective pressures. However, a caveat was introduced by Shi, Bakewell, and Zhang (2006), who argued that accelerated evolution might not be a feature of many genes expressed in brain tissue, and that results obtained in this kind of study might be biased by the criterion used to include specific genes in the study, as well as the composition of the outgroups used for comparison.

Thus, the origins and evolution of aesthetic appreciation, as well as other characteristically human cognitive mechanisms, might not owe solely to increases in the relative sizes of certain neocortical regions per se, but also to the timing of their development. The normal maturation of neural circuits requires a precise developmental timing and the organism's interaction with its environment. This has been shown by Majdan and Shatz' (2006) study of the effects of visual deprivation on gene expression during the development of the visual cortex in mice, among many others. The authors reported that the regulation of some genes involved in the maturation of neural circuitry is dependent on the history of sensory experience, suggesting an intricate relation between environmental stimulation and gene expression in the development of the neural substrates of visual processing.

Changeux (2005) reviewed some of the evidence showing that the developmental phases in which the maximum number of synapses is achieved and then trimmed are unusually long in humans. This is a crucial point, given the importance of connectivity in understanding human brain evolution. Changeux (2005) noted that the increase of cerebral-cortex surface affords the possibility of creating a larger amount of connections among neurons. And an increase in connectivity would lead to a greater arborization of dendrites and axons, which is precisely what is observed in the prefrontal cortex when compared with other brain regions, such as the primary visual cortex. Whereas earlier phases are relatively insensitive to environmental influence, these extended periods, which last throughout human infancy, are especially sensitive to external information. Hence, the brain of human beings is influenced by external factors at a crucial stage in development—when neural connections are being forged, strengthened, or eliminated.

Brain epigenetic capacities to store stable representations of the outside world give human beings the opportunity to create an artificial world of cultural objects at the social level. In other words, the origin of culture and of its transmission from generation to generation lies in the considerable increase of synapse numbers and multiple nested processes of activity-dependent synapse selection that take place postnatally in the human brain. This epigenetic evolution also has another consequence: it permits the diversification of cultures that human beings have developed throughout their recent history. In other words, the postnatal epigenetic evolution of brain connectivity opens the way to cultural evolution (Changeux, 2005, p. 89).

Hence, the malleability of neural connectivity at early stages of development makes the human brain especially susceptible to environmental influences. In the case of humans, though, an important part of this environment is constituted by cultural elements. Laland, Odling-Smee, and Feldman (2001) summarized a large body of work showing the important role of the creation of a cultural environment throughout human evolution. Just as humans grow up surrounded by biological elements, such as certain plants, animals, climate, and so on, they also develop in a rich cultural surrounding, which includes language, social interactions, and the use of colors, shapes, objects, movements, and sounds, among other features, for aesthetic purposes. Obviously, the cultural milieu in which we grew up did not appear suddenly in human evolution. It is the result of a slow and gradual accumulation of cultural practices and traditions. Tomasello (1999), who described this process as "the ratchet effect" has argued that social learning skills and innovation are the base of cumulative cultural evolution. Children's imitative learning from adults assures that the cultural practices will not be lost from one generation to the next. On the other hand, innovation allows more effective novel cultural variants to be transmitted to future generations. Thus, each generation does not need to create cultural elements from scratch, they modify those they learned from their parents and will transmit those modifications to their own children. In the case of aesthetic appreciation, generation after generation, humans increased the sophistication and broadened the variation of aesthetic expression, creating many new forms of providing aesthetic pleasure. These, in turn, became the cultural environment in which a new generation would be immersed, and, according to the literature reviewed above, may have influenced certain aspects of the organization of neural development and connectivity. Lewontin (1990) emphasized the need to study cognitive traits both as the consequence and cause of evolution, just as any other kind of traits. Hence, paraphrasing Lewontin (1990), evolutionary approaches need to study the evolution of such phenomena as aesthetic preference and creativity, as well as their consequences on human evolution. The way in which this reciprocal influence between biological and cultural evolution has affected aesthetic appreciation has yet to be systematically explored.

CONCLUSIONS: TOWARD A FRAMEWORK FOR THE EVOLUTION OF AESTHETIC PREFERENCE

We have assembled a collection of diverse bits and pieces in this chapter. We will now briefly sketch some of the implications of these pieces for hypotheses concerning the evolution of aesthetic preference, as if we were laying down some of the side pieces of a jigsaw puzzle without knowing many of details of the final image. But before we do so, we wish to acknowledge two of the most important limitations of the present work. First, in our review of comparative neurology, we have focused on the higher levels of brain organization. This is because comparative data at the lower levels are scarce, and not because we believe they are less important for the question at hand. Second, although in some instances we have assumed a correspondence between anatomical and cognitive change,

there is a daunting lack of knowledge about the cognitive impact of neuro-anatomical changes during evolution. In spite of these two shortcomings, we believe the following conclusions represent valuable constraints for evolutionary approaches to aesthetic preference, and even possibly to other related phenomena, such as creativity.

Aesthetic preference is the result of the interaction of several component cognitive processes. This fact has been reflected in recent cognitive models based on a large corpus of psychological and neuropsychological studies (Chatterjee, 2003; Leder et al., 2004). Neuroimaging studies have confirmed that there is no single brain center for aesthetic preference, and that different component processes are associated with activity in different brain regions. The reward value of aesthetically pleasing visual stimuli seems to be represented in the orbitofrontal cortex (Kawabata & Zeki, 2004) and caudate nucleus (Vartanian & Goel, 2004). It has been argued that the anterior cingulate cortex, the activity of which was recorded by Vartanian and Goel (2004) and Jacobsen and colleagues (2005) during aesthetic preference tasks, is involved in the conscious awareness of emotional processes. Attentional or emotional mechanisms engaged by preferred stimuli enhance early visual processes in the occipital cortex (Vartanian & Goel, 2004). Activity in the temporal pole seems to provide an emotional and mnemonic context for decisions about beauty (Jacobsen et al., 2005). And, finally, making decisions about the beauty of visual stimuli has been associated with activity in frontopolar and lateral prefrontal regions (Cela-Conde et al., 2004; Jacobsen et al., 2005). It is a certain temporal and spatial distribution of neural activity that enables each human to enjoy viewing certain artworks and designs but not others. Hence, the question of the evolution of aesthetic preference becomes the question of the evolutionary history of those components, their neural bases, and their interaction.

A consequence of shifting our focus to the component processes is that their evolution might be relatively independent. The possibility that they may have different origins is opened. Also, comparative studies become a powerful tool to determine their putative precursors. In fact, our review has shown that, to a very large extent, the component cognitive processes, as well as their neural bases, are present in our close living relatives. Hence, we can assume that they were also present in the common ancestors of humans and monkeys. According to the parsi-monious criterion underlying modern phylogenetic reasoning, this is a much likelier scenario than assuming they appeared independently in two closely related lineages. It would seem, therefore, that aesthetic preference has evolved through the recruitment of preexisting cognitive processes and neural structures, rather than by substantive changes in brain and cognition.

This does not mean that there has been no modification of cognitive processes and neural structure during human evolution. We mean to say that humans acquired aesthetic preference by virtue of gradual and quantitative changes in certain brain regions. Specifically, an increase in the complexity of prefrontal connectivity patterns, the elaboration of the dorsal visual stream, together with cytoarchitec-tonic novelties in the anterior cingulate cortex. Presumably, these modifications afforded a richer integration of multimodal information and the generation of

abstract representations, an improved analysis of spatial relations, together with a heightened ability for cognitive control, respectively.

These changes in the brain bases of aesthetic preference may have occurred at different times throughout human evolution. Furthermore, they might have been driven by diverse selective pressures, which need not have been related to aesthetic preference originally. Hence, evolutionary approaches to this human experience can, and probably must, include more than one hypothesized selective advantage, and even evolutionary mechanism.

The development of connectivity patterns in the human brain is sensitive to environmental factors. It is possible that this increased plasticity has played a relevant role in the evolution of aesthetic preference. At least during the last 200,000 years the exposure of human infants to diverse cultural practices, including those designed to embellish the environment—body painting, ornamental objects, bone carving, and so on—has surely been a keynote aspect in the development of an aesthetically tuned mind. The cultural production of aesthetic elements has been slow and gradual, with many different local traditions and forms of expression. Evolutionary approaches to aesthetic preference need to account for the interplay between cultural and biological evolution.

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