

BRAIN INTERSECTIONS OF AESTHETICS AND MORALS

*perspectives from biology, neuroscience,
and evolution*

D. W. ZAIDEL* AND M. NADAL†

ABSTRACT For centuries, only philosophers debated the relationship between aesthetics and morality. Recently, with advances in neuroscience, the debate has moved to include the brain and an evolved neural underpinning linking aesthetic reactions and moral judgment. Biological survival emphasizes mate selection strategies, and the ritual displays have been linked to human aesthetics in the arts, in faces, and in various daily decision making. In parallel, cultural human practices have evolved to emphasize altruism and morality. This article explores the biological background and discusses the neuroscientific evidence for shared brain pathways for aesthetics and morals.

HUMAN AESTHETIC EXPERIENCES are pervasive; they are triggered by faces, art, natural scenery, foods, ideas, theories, and decision-making situations, among many sources, and seem to be a distinctive trait of our species. Our moral sense, understood as our capacity to judge events, actions, or people as good or bad, appropriate or inappropriate, also seems to be an exclusively human endow-

*Department of Psychology, University of California at Los Angeles (UCLA).

†Human Evolution and Cognition Group (IFISC-CSIC), University of the Balearic Islands, Mallorca, Spain.

Correspondence: Dr. D. W. Zaidel, Department of Psychology, UCLA, Box 951563, Los Angeles, CA 90095-1563.

E-mail: dahliaz@ucla.edu.

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ment (Ayala 2010). As part of the scientific efforts to characterize the biological foundations of our human uniqueness, recently there has been interest in the brain's underpinnings of aesthetic reactions to art on the one hand, and in the neural correlates of moral judgment and decision-making on the other (Greene and Paxton 2009; Harenski et al. 2010; Höfel and Jacobsen 2007; Moll et al. 2005; Nadal et al. 2008; Skov 2009).

Most people commonly think of morality as dealing with right and wrong and of aesthetics as dealing with beauty issues. At first glance, these concepts seem like apples and oranges, so widely apart as not to be related at all in the human cultural fruit bowl. However, two different connections, one between art and ethics, and the other between beauty and goodness, sink their roots deep into the western history of philosophy and were explored by some of the great modern philosophers, like Hume and Kant.

The ethical approach to artworks was strongly influenced by the work of Plato, especially *The Republic*. Good art, according to Plato, should be created in agreement with the laws of the cosmos, and it should mould people's characters in accordance to the idea of good. He approved of archaic Greek and Egyptian art because he believed that they served truth and the strengthening of character. In contrast, he condemned the art of his time for presenting a distorted or superficial—and thus false—image of reality. He also condemned art for corrupting by stimulating people's feelings, and thereby debilitating their character and moral diligence (Tatarkiewicz 1970). Philosophers have tackled such issues throughout history, and continue to do so today (Schellekens 2007), especially with regards to the questionable ethical content of some contemporary artworks, such as those that extol ethnic superiority, violence, sexism, and so on. Moreover, the concern for ethical issues in art is by no means restricted to the Western tradition. The Yoruba people of West Africa, for instance, use physical beauty in sculpture to convey their highest ethical values (Anderson 2004).

A related but different association, the one linking the notions of beauty and good, is probably even more deep-seated in Western thought. In early Greek thinking, beauty was a much broader concept than in our own age, and it was used to refer to all that was liked for its form and structure or that awakened admiration. It could encompass sounds and images, but also the character traits that constitute moral beauty (Tatarkiewicz 1970). The Pythagoreans, the first to deal with aesthetics from a philosophical perspective, grounded their thinking on the concept of harmony, which was necessarily both beautiful and positive. The Sophists narrowed this ancient concept, creating a notion of beauty that was free from moral connotations. Later thinkers, including Plato and Aristotle, conceived beauty only in its aesthetic sense, but Stoic philosophers, who also maintained such a division, actually regarded moral beauty as a better representative of beauty itself than its aesthetic counterpart. Thus, Chrysippus wrote: "Since a thing is good it is beautiful; now it is beautiful, therefore it is good" (cited in Tatarkiewicz 1970). Similar views surfaced repeatedly in the thinking of philoso-

phers and artists in later centuries. An example is a particular portraiture style practiced in the Renaissance: a woman's beauty was equated with the good, virtuous, and socially moral, so artists painted them as beautiful in order to depict those high-level virtues (Brown 2003). The link between beauty and good is so ingrained in our present conventional thinking that it is often experienced in our daily life. Psychologists have shown that in many different settings people tend to judge and treat attractive children and adults better than their unattractive peers (Langlois et al. 2000).

Scientists are only just beginning to explore the neurobiological foundations that bond beauty and goodness in the minds of humans. Agnati and colleagues (2007) theorized that certain neural networks in the human brain that are intimately linked with the limbic system might encode ethical and aesthetic principles. Tsukiura and Cabeza (2010) recently explored this connection empirically. In order to determine whether there is an overlap between brain regions involved in judgments of beauty and morality, they used functional magnetic resonance imaging (fMRI) to register their participants' brain activity while performing facial attractiveness and goodness judgments. Their results showed that neural processes in the orbitofrontal and insular cortices, related with the representation of reward value and emotional states, contribute to both kinds of judgment.

In this article, we extend this line of reasoning with the conviction that neuroscientific and evolutionary approaches to human aesthetic and moral behavior provide new and fruitful insights into the links between them. To examine the shared underpinnings, we first explore specific biological strategies that maximize organisms' fitness, namely morality and mate selection displays, and then look to neuroscience to uncover the related intersections. As the ensuing discussion will attempt to show, it is no coincidence that philosophers paid attention to the ties between beauty and goodness, for the origins of the biological mechanisms subserving the assessment of these human values can be traced to our biological animal ancestry, and their interrelationship to shared neural pathways in the brain.

BIOLOGICAL EXPLANATIONS FOR MORALITY AND AESTHETICS

As biological organisms we have inherited a myriad of physiological, psychological, genetic, and survival predispositions from our animal ancestors. These predispositions have taken on new modes of expression given our *Homo sapiens* brain's heavy reliance on symbolic communication and cultural practices, which include moral and aesthetic issues.

Ancestral Roots of Morality

Ayala (2010) has defined morality as "the urge or predisposition to judge human actions as either right or wrong in terms of their consequences for other human beings" (Ayala, 2010, p. 9018). Moral behavior is sometimes instinctual

and sometimes explicitly taught, dictated, shaped by religion, school, and family, and has adaptive survival advantages for society (Miller 2007). However, whereas the particular moral codes according to which actions are judged vary across societies and are a product of cultural evolution, morality is inherent to human nature. This is because, as Ayala (2010) has put it, human biological constitution includes all the necessary cognitive mechanisms for morality. The question, therefore, is to determine how these constituents became intrinsic to our nature.

Evolutionary biologists have suggested that human predispositions for morality were laid down through the same evolutionary mechanisms as social behaviors in many other species. The evolution of altruistic behaviors in several organisms, including humans, is a paradigmatic example of such mechanisms. Why should an organism decrease its survival and reproduction chances to favor another individual? Hamilton (1964) suggested that, given that related kin share copies of many different genes, individuals are able to increase the frequency of those genes in subsequent generations by aiding close relatives in survival and reproduction. But what about altruism among unrelated organisms? Trivers (1971) introduced the notion of reciprocal altruism to suggest that altruistic behavior among unrelated organisms might be selected when individuals interact for long periods of time, and when the probabilities of reciprocating altruistic behaviors are high. Our species' morality resulted from these and other mechanisms acting upon a long ancestry of highly social primate species.

Converging evidence from comparative psychology has also revealed evidence that the cognitive mechanisms that underlie human morality were inherited from distant primate ancestors. Morally related behaviors that humans interpret to be fairness, revenge, consolation, reconciliation, conflict mediation, or cheating and deviousness are observed with various degrees of expression in non-primates, all in the service of survival and reproductive success (Byrne and Whiten 1992; de Waal 1982; Hauser 2006). Moreover, there is evidence that nonhuman primates, especially apes, possess some of the building blocks of human morality, including the ability to distinguish between self and others, empathy, internalization of rules, and anticipation of punishment (Flack and de Waal 2000).

Ancestral Roots of Aesthetics

According to some views, our sense of aesthetics can be traced through our biological ancestry to mate choice and its associated courtship rituals (Miller 2000; Zahavi 1978), although there is no direct evidence that animals experience aesthetics in the course of their own courtship rituals. What is key here is the display itself: organisms use a myriad of strategies to attract potential mates through displays of the genetic goods in order to propagate successfully (Cronin 1992). In the service of survival of the species, elaborate courtship displays evolved with great biological investment to attract observation and assessment by potential mates. The displayed signals are meant to convey health status, strength,

genetic, and fitness quality. The case of the peacock and the peahen is classic by now: the peacock has evolved an elaborately ornate tail over and above what it needs to fly or avoid predators. To attract a would-be mate, the peacock lifts and fans out his tail while strutting in front of the peahen, who assesses the display for various imperfections emanating from physical defects, disease, deviations from symmetry, and other clues to health and fitness; imperfections could genetically minimize the survival options of her offspring. The effect is bidirectional: the attracting male and the reciprocating female share underlying brain neuronal wiring. In this regard, human aesthetics is not dissimilar: aesthetic judgment is associated attention to the message in the assessed object (Miller 2000). Humans also use aesthetics to lure, entice, and con, as is particularly evident in mass-media advertising strategies (discussed subsequently). Aesthetics, however, has evolved to take on a broader role for humans, particularly as it applies to various forms of symbolic thinking and communication.

Human Moral and Aesthetic Culture: Art, Mate Choice, Decision Making

Three aesthetic-related behaviors and their intersections with morals will be considered here, namely art, human mate selection, and personality. The view adopted here is that aesthetics serve as a means to assess a “display of the goods,” where the behavior resulting from the assessment sometimes falls on a moral continuum. Art is a uniquely human endeavor: it is practiced in all human societies throughout the world and does not seem to have a direct utilitarian or economic value. It is a prime example of symbolic expression and communication. Art entices us through its aesthetics to consider its symbolic or referential representation, even when emotionally unbearable material is depicted. Disturbing, jarring subject matter, which if experienced in real time would repulse or frighten and most certainly would not elicit an aesthetic response, may in fact elicit an aesthetic response when viewed on canvas. The very enticement opens the door to the morality issue, as the aesthetics of the art entices us despite its theme. For example, Francisco de Goya’s *The Third of May* depicts war atrocities during the Napoleonic War in 1808, yet it generates profound aesthetic reactions and is considered to be first-rate art. Through its aesthetics, the artwork attracts us into looking at the morally “unthinkable” and to cognitively consider emotionally unbearable subjects. In this regard, the displayed art is a tool for ensnaring, luring, and enticing our attention so as to make its thematic message effective.

There is another way in which the aesthetics in art can “hoodwink” us. Art reflects the cognitive and genetic skill, creativity, and talent of the artist. In this sense, art provides a platform to exhibit these qualities. Yet aesthetics can entice us to art even when it is created by artists whose visual or auditory health was severely compromised (see Zaidel 2005). Claude Monet was practically blind because of bilateral cataracts when he created the famous water lilies paintings; Edward Degas suffered from monocular blindness when he created most of his famous ballerina paintings; Paul Cezanne suffered from myopia throughout most

of his life. Beethoven was deaf when he wrote his famous symphonies. We are enticed through the aesthetics of the art and react to the display of good genes controlling artistic intelligence, skill, and creativity rather than to genes controlling the physical health of the producer. In such instances, symbolic cognition, the hallmark of the human brain, takes precedence over displays of physical health, the latter being critical for animal survival, not for human survival.

Similarly, with human mate choice, across many cultures the selection is heavily dependent on female attractiveness and beauty: Buss (1989) notes that a woman's beauty is a common priority in 37 different cultures. Beauty is a strong attractant for permanent mating, and it can mask other requisite qualities for human survival, such as long-term investment in the young and family unit, dependability, empathy, and loyalty. Yet human facial beauty, per se, does not necessarily predict perfection, good health and good genes (Kalick et al. 1998; Weeden and Sabini 2005). Indeed, what we humans call beautiful may be unrelated to those qualities that are so critical for animal survival; our cultural practices, symbolic cognition, and social interactions have subordinated and altered these qualities. Although interpersonal features would be much more practical for long-term human survival, aesthetics still plays a critical role in choosing a procreating partner, like a leftover functional appendage from our animal biological ancestors.

Indeed, physical beauty in both males and females can be deceiving in more ways than one. Helen of Troy's beauty is said to have "launched a thousand ships" and triggered the bloody war between Troy and Sparta. Psychologists have long studied the influence of facial beauty on decision making in social, non-mating situations, including business, marketing, and advertising, and the effects of beauty on behavior have proven powerful in profound ways. Physically attractive people are perceived as being endowed with positive traits such as trust, intelligence, and competence (Veenvliet and Paunonen 2005); they receive better treatments than unattractive people, including in court criminal cases (Sigall and Ostrove 1975); and teachers have been shown to favor attractive children through giving attention and assigning high grades (Rich 1975). Advertisers have consciously applied the power of beauty through the use of attractive women and men to entice us to engage in activities that are not necessarily good for us and that could in fact be considered amoral, from smoking cigarettes, eating potato chips, and thinking we are losing weight, to eating yogurt and thinking it makes us healthy because it contains fruit, to taking unnecessary medication to make us virile, disease-free, or pain-free, despite myriad dangerous side effects. The conscious use of aesthetics to lure, con, or entice has moral implications. In sum, humans are morally susceptible to what is metaphorically described as the "power of beauty."

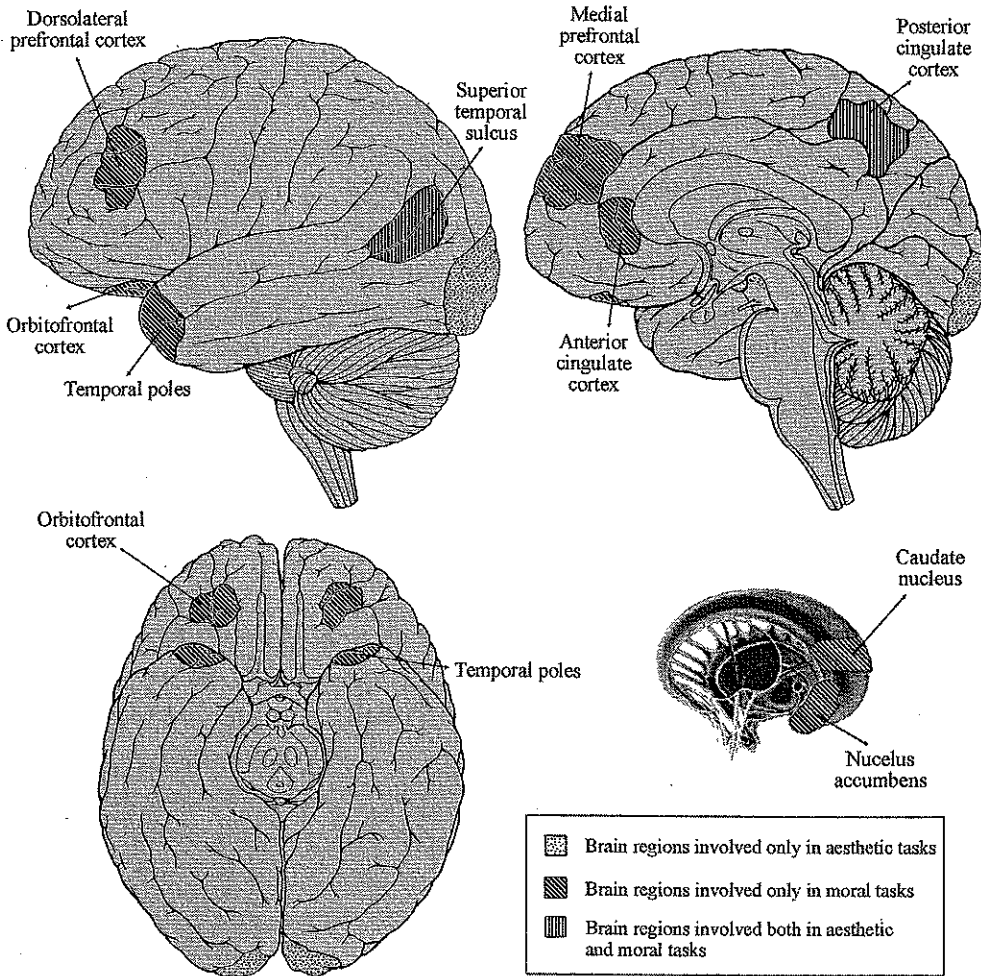


FIGURE 1

Overlapping functional networks in human brain regions involved in aesthetic and moral tasks.

NEUROSCIENCE AND AESTHETICS AND MORALS

So, can neuroscience explain the profound effects that aesthetics and morality have on human behavior? What is actually known about the neurobiological mechanisms involved in processing goodness and beauty? Neuroimaging studies during the last decade have revealed that moral reasoning or aesthetic appreciation rely on activity distributed across multiple cortical and subcortical brain regions, rather than on a single especially dedicated neural mechanism.

Brain Regions Involved in Moral Cognition

Even the simplest moral task, such as reading statements with moral connotations, engages a suite of regions throughout the brain (see Figure 1). Activity in the superior temporal sulcus has been interpreted as reflecting emotional processing in the context of perceived social signs and theory of mind. Activity in the posterior cingulate cortex and precuneus is thought to be associated with the integration of cognitive control and affective processes, especially when overcoming

conflict, together with the anterior cingulate cortex. The role of the medial prefrontal cortex seems to be especially relevant when moral tasks require considerable cognitive control and decision making in relation to reward and punishment, as well as self-referential processing. Temporal pole activity is considered to underlie the integration of moral knowledge with emotions that determine the reinforcing value of actions. The involvement of the dorsolateral orbitofrontal cortex in moral tasks is assumed to reflect cognitive control, monitoring of task performance, and active retrieval from working memory. Finally, activity in the orbitofrontal cortex has been related to the integration of cognitive and affective processes and the processing of rewards (Greene and Paxton 2009; Greene et al. 2004; Moll et al. 2005; Schaich-Borg et al. 2007; Young et al. 2007).

Brain Regions Involved in Aesthetic Appreciation

Recent neuroimaging studies have also identified activity in diverse brain regions in the context of aesthetic valuation of paintings, photographs, architecture, music, and dance. The studies suggest that aesthetic valuation involves three kinds of brain activity (Nadal and Pearce 2011). First, aesthetic valuation causes an enhancement of low- and mid-level cortical visual, auditory, and somatosensory processing, presumably reflecting the engagement of attentional or affective processes (Calvo-Merino et al. 2010; Cela-Conde et al. 2009; Cupchik et al. 2009; Vartanian and Goel 2004). Second, high-level top-down processing and activation of cortical areas are involved in evaluative judgment, including the anterior medial prefrontal cortex and the ventral and dorsal aspects of the lateral prefrontal cortex (Cela-Conde et al. 2004; Cupchik et al. 2009; Jacobsen et al. 2006). Finally, aesthetic valuation engages the reward circuit, including cortical (anterior cingulate, orbitofrontal, and ventromedial prefrontal) and subcortical (caudate nucleus, substantia nigra, and nucleus accumbens) regions, as well as some of the regulators of this circuit (amygdala, thalamus, hippocampus; Blood and Zatorre 2001; Cupchik et al. 2009; Ishai 2007; Kawabata and Zeki 2004; Kirk et al. 2009; Vartanian and Goel 2004).

Neurobiological Connections Between Aesthetic Appreciation and Moral Cognition

None of the brain regions that constitute the networks associated with moral or aesthetic judgments are exclusively dedicated to these domains. They are all engaged in tasks related to diverse spheres of human experience, though they seem to contribute with similar computations across all of them. Moreover, the fact that the identified regions vary from one experiment to another, both for morals and aesthetics, suggests that the demands of different moral tasks, such as solving moral dilemmas, viewing scenes with moral content, reading sentences conveying guilt, or judging the permissibility of another's actions, rely on partially overlapping subsets of the regions described above. The same can be said

of different aesthetic tasks, such as deciding how beautiful or attractive an object is, or how much one likes or prefers it.

Especially interesting for the aims of this article is the degree of overlap between the functional networks of brain regions underlying beauty appreciation and moral reasoning. Both seem to involve the following common elements: executive functions, such as attention, working memory, and decision making, associated with activity in the medial and lateral prefrontal cortex; the representation and anticipation of reward value, which is usually related with orbito-frontal activity; the creation of an emotion-rich context based on memories of past experiences, involving the temporal poles; and the integration of affective and cognitive processes in the anterior cingulate cortex. In the case of moral tasks, this network is complemented by activity in brain regions associated with social cognition (superior temporal sulcus) and the integration of cognitive conflict and emotion (posterior cingulate cortex and precuneus). In addition to the common neural network, aesthetic valuation tasks also engage low- and mid-level sensory processes (visual, auditory, and somatosensory cortices, depending on the form of art) and the reward system (especially the ventral striatum).

Philosophers have never come to an agreement as to the exact nature of the relationship between good and beauty in our surrounding reality, especially in other people—or as to whether such a relationship actually exists. Neuroscience, however, is beginning to show that our capacities to recognize beauty and goodness are mediated by partially overlapping neural networks. These common neurobiological mechanisms may actually be what bonds such values in our minds.

We have already mentioned that brain regions constituting these networks are also involved in decisions related to other domains. But what makes the aforementioned association particularly interesting is that it concerns human values that people around the world hold very dearly, and probably have done ever since the origins of our species, judging from the decorative, funerary, and paleopathological evidence in the archaeological record. The possession of moral and aesthetic values is distinctively human, as are the efforts, resources, and costs we spend and invest to uphold them. Thus, two of the traits that define our humanity—our moral and aesthetic attitudes towards our physical and social environment—are grounded in part on common neural mechanisms. This fact is of enormous relevance to understanding the evolutionary origins of such uniquely human traits.

EVOLUTIONARY TIES BETWEEN AESTHETICS AND MORALS

The fact that no other animal seems to come close to exhibiting such sophisticated and varied moral and aesthetic processes as we do would suggest that their biological underpinnings evolved after the human and chimpanzee lineages split. In addition to some conspicuous differences, however, comparative neuroanat-

omy has revealed striking cytoarchitectonic and connectivity parallels between humans and other primates within and between the brain regions involved in both aesthetic and moral judgments. These commonalities refer to aspects of the cytoarchitecture and functions of the lateral, anterior, and orbital prefrontal cortices and the temporal poles; the involvement of the superior temporal sulcus in social reasoning and representation of conspecifics; the cytoarchitecture of the precuneus; and the retinotopic organization of primary and secondary visual areas; as well as the representation of objects and the processing of symmetry (Bell et al. 2009; Cavanna and Trimble 2006; Leichnetz 2001; Orban, Van Essen, and Vanduffel 2004, Petrides 2005; Semendeferi et al. 2001). Such similarities suggest that these features have not been significantly altered and were not under strong selective pressures during human evolution.

On the other hand, certain features of the common neural underpinnings of morals and aesthetics 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 diversity of sensory modalities; the cytoarchitectural organization of the anterior cingulate cortex has been significantly reconfigured; the precuneus has expanded and grown in organizational complexity; 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, and Procyk 2005; Denys et al. 2004; Holt, Graybiel, and Saper 1997; Leichnetz 2001; Nimchinsky et al. 1999; Orban, Van Essen, and Vanduffel 2004; Semendeferi et al. 1998, 2001; Vogt et al. 1995). These evolutionary developments afforded humans the following selective advantages: the capacity to elaborate information to produce abstract representations, symbols, which are not necessarily tied to sensory modalities or related with real entities; enhanced supervision of information processing and conflict monitoring and resolution; sophisticated processing of visual spatial relations; and increased regulation and self-awareness of affective and emotional states.

The basic constituents of the neural networks that underlie aesthetic valuation and moral judgment, therefore, were inherited from our distant primate ancestors. However, specific alterations to certain brain regions involved in our capacity to assess both goodness and beauty, 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 was a single evolutionary event that altered them in a manner critically representing a clear-cut stage shift. Rather, gradual changes throughout the human lineage, and probably owing to diverse selective pressures—such as social interactions between family and non-family

members, increased group size, hierarchical organization, and climatic changes—are likely to have occurred (Henshilwood and Marean 2003; McBrearty and Stringer 2007; Varki, Geschwind, and Eichler 2008).

Moreover, evolutionary adaptive modifications to the common neural network were surely not only relevant to these domains: all of the brain regions discussed here are involved in a number of other human cognition and behaviors as well. Hence, it is conceivable that some brain modifications leading to our capacity to perform moral judgments and aesthetic valuations were not selected for the advantages conferred by either one alone. In this scenario, then, the notion of shared brain regions for several forms of cognition is a likely possibility (Cruse 2003).

CONCLUSION

Neuroscience is now in a position to add to the centuries-old debates about beauty and the morally good in people, their actions, and objects, by showing that the bond between beauty and good may reside in the intimate neurobiological and evolutionary relations between the mechanisms we rely on to assess these values.

It is not unreasonable to propose that the functions of aesthetics and morals share common neural networks. Multipurpose brain regions and functional redundancy could support such an intersection. One possible mechanism by which cognitive functions can be supported by the same brain region is redeployment. Anderson (2007) suggests that brain regions that originally served a single biological function have evolved through adaptive pressures to serve more than one function—indeed, diverse functions. Gould and Vrba (1982) discussed the notion of exaptation, whereby behavioral functions could be present through the biological ancestry but not necessarily created anew through selective adaptive pressures. The shared neural pathways of aesthetics and morals could be explained by either one of these notions, or by both.

Given our *Homo sapiens* brain with its heavy reliance on symbolic communication, cultural, and ritualistic practices, we would expect similarities among behaviors relying on abstract cognition (Zaidel 2010). The fact that aesthetics and morals rely on a set of common brain regions supports the notion that some neural modifications and selective pressures applied to both in early human experience. The survival pressures would stem from an increase in social group size, critical cooperation, and altruism among non-family members, as well as developed cultural practices promoting cohesion (Bell 2010). All of these could have been major contributors to the mingling of aesthetic preference and moral judgment.

REFERENCES

- Agnati, L. F., et al. 2007. Does the human brain have unique genetically determined networks coding logical and ethical principles and aesthetics? From Plato to novel mirror networks. *Brain Res Rev* 55:68–77.
- Amiez, C., J.-P. Joseph, and E. Procyk. 2005. Primate anterior cingulate cortex and adaptation of behavior. In *From monkey brain to human brain*, ed. S. Duhamel, M. D. Hauser, G. Rizzolatti, 315–36. Cambridge: MIT Press.
- Anderson, M. L. 2007. Evolution of cognitive function via redeployment of brain areas. *Neuroscientist* 13:13–21.
- Anderson, R. A. 2004. *Calliope's sisters: A comparative study of philosophies of art*, 2nd ed. Upper Saddle River, NJ: Pearson Prentice Hall.
- Ayala, F. J. 2010. The difference of being human: Morality. *Proc Natl Acad Sci USA* 107: 9015–22.
- Bell, A. H., et al. 2009. Object representations in the temporal cortex of monkeys and humans as revealed by functional magnetic resonance imaging. *J Neurophysiol* 101: 688–700.
- Bell, A. V. 2010. Why cultural and genetic group selection are unequal partners in the evolution of human behavior. *Commun Integr Biol* 3:159–61.
- Blood, A. J., and R. J. Zatorre. 2001. Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. *Proc Natl Acad Sci USA* 98:11818–823.
- Brown, D. A. 2003. *Virtue and beauty: Leonardo's Ginevra de Benci and Renaissance portraits of women*. Princeton: Princeton Univ. Press.
- Buss, D. M. 1989. Sex differences in human mate preferences: Evolutionary hypotheses testing in 37 cultures. *Behav Brain Sci* 12:1–49.
- Byrne, R. W., and A. Whiten. 1992. Cognitive evolution in primates: Evidence from tactical deception in primates. *Man* 27:609–27.
- Calvo-Merino, B., et al. 2010. Extrastriate body area underlies aesthetic evaluation of body stimuli. *Exp Brain Res* 204:447–56.
- Cavanna, A. E., and M. R. Trimble. 2006. The precuneus: A review of its functional anatomy and behavioural correlates. *Brain* 129:564–83.
- Cela-Conde, C. J., et al. 2004. Activation of the prefrontal cortex in the human visual aesthetic perception. *Proc Natl Acad Sci USA* 101:6321–25.
- Cela-Conde, C. J., et al. 2009. Sex-related similarities and differences in the neural correlates of beauty. *Proc Natl Acad Sci USA* 106:3847–52.
- Cronin, H. 1992. *The ant and the peacock*. Cambridge: Cambridge Univ. Press.
- Cruse, H. 2003. The evolution of cognition: A hypothesis. *Cogn Sci* 27:135–55.
- Cupchik, G. C., et al. 2009. Viewing artworks: Contributions of cognitive control and perceptual facilitation to aesthetic experience. *Brain Cogn* 70:84–91.
- de Waal, F. B. 1982. *Chimpanzee politics*. New York: Harper and Row.
- Denys, K., et al. 2004. Visual activation in prefrontal cortex is stronger in monkeys than in humans. *J Cog Neurosci* 16:1505–16.
- Flack, J. C., and F. B. de Waal. 2000. "Any animal whatever": Darwinian building blocks of morality in monkeys and apes. *J Conscious Stud* 7:1–29.
- Gould, S. J., and E. S. Vrba. 1982. Exaptation: A missing term in the science of form. *Paleobiology* 8:4–15.

- Greene, J. D. and J. M. Paxton. 2009. Patterns of neural activity associated with honest and dishonest moral decisions. *Proc Natl Acad Sci USA* 106:12506–511.
- Greene, J. D., et al. 2004. The neural bases of cognitive conflict and control in moral judgment. *Neuron* 44:389–400.
- Hamilton, W. 1964. The genetical evolution of social behaviour: I. *J Theor Biol* 7:1–16.
- Harenski, C. L., et al. 2010. A functional imaging investigation of moral deliberation and moral intuition. *Neuroimage* 49:2707–16.
- Hauser, M. D. 2006. *Moral minds: How nature designed our universal sense of right and wrong*. New York: Harper Collins.
- Henshilwood, C. S., and C. W. Marean. 2003. The origin of modern human behavior. *Curr Anthropol* 44:627–51.
- Höfel, L., and T. Jacobsen. 2007. Electrophysiological indices of processing aesthetics: Spontaneous or intentional processes. *Int J Psychophysiol* 65:20–31.
- Holt, D. J., A. M. Graybiel, and C. B. Saper. 1997. Neurochemical architecture of the human striatum. *J Comp Neurol* 384:1–25.
- Ishai, A. 2007. Sex, beauty and the orbitofrontal cortex. *Int J Psychophysiol* 63:181–85.
- Jacobsen, T., et al. 2006. Brain correlates of aesthetic judgment of beauty. *Neuroimage* 29: 276–85.
- Kalick, S. M., et al. 1998. Does human facial attractiveness honestly advertise health? Longitudinal data on an evolutionary question. *Psychol Sci* 9:8–13.
- Kawabata, H. and S. Zeki. 2004. Neural correlates of beauty. *J Neurophysiol* 91:1699–1705.
- Kirk, U., et al. 2009. Brain correlates of aesthetic expertise: A parametric fMRI study. *Brain Cogn* 69:306–15.
- Langlois, J. H., et al. 2000. Maxims or myths of beauty? A meta-analytic and theoretical review. *Psychol Bull* 126:390–423.
- Leichnetz, G. R. 2001. Connections of the medial posterior parietal cortex (Area 7m) in the monkey. *Anat Rec* 263:215–36.
- McBrearty, S., and C. Stringer. 2007. The coast in colour. *Nature* 449:793–94.
- Miller, G. F. 2000. *The mating mind: How sexual choice shaped the evolution of human nature*. New York: Doubleday.
- Miller, G. F. 2007. Sexual selection for moral virtues. *Q Rev Bio* 82:97–125.
- Moll, J., et al. 2005. Functional networks in emotional moral and nonmoral social judgments. *Nat Rev Neurosci* 6:799–809.
- Nadal, M., and M. T. Pearce. 2011. The Copenhagen Neuroaesthetics Conference: Prospects and pitfalls for an emerging field. *Brain Cogn* 76:172–83.
- Nadal, M., et al. 2008. Towards a framework for the study of the neural correlates of aesthetic preference. *Spat Vis* 21:379–96.
- Nimchinsky, E. A., et al. 1999. A neuronal morphologic type unique to humans and great apes. *Proc Natl Acad Sci USA* 96:5268–73.
- Orban G. A., D. Van Essen, and W. Vanduffel. 2004. Comparative mapping of higher visual areas in monkeys and humans. *Trends Cogn Sci* 8:315–24.
- Petrides, M. 2005. Lateral prefrontal cortex: Architectonic and functional organization. *Philos Trans R Soc Lond B* 360:781–95.
- Rich, J. 1975. Effects of children's physical attractiveness on teachers' evaluations. *J Educ Psychol* 67:599–609.

- Schaich-Borg, J., et al. 2007. Consequences, action, and intention as factors in moral judgments: An fMRI investigation. *J Cogn Neurosci* 18:803–17.
- Schellekens, E. 2007. *Aesthetics and morality*. New York: Continuum.
- Semendeferi, K., et al. 1998. Limbic frontal cortex in hominoids: A comparative study of area 13. *Am J Phys Anthropol* 106:129–55.
- Semendeferi, K., et al. 2001. Prefrontal cortex in humans and apes: A comparative study of area 10. *Am J Phys Anthropol* 114:224–41.
- Sigall, H., and N. Ostrove. 1975. Beautiful but dangerous: Effects of offender attractiveness and nature of the crime on juridic judgment. *J Perspect Soc Psychol* 31:410–14.
- Skov, M. 2009. Neuroaesthetic problems: A framework for neuroaesthetic research. In *Neuroaesthetics*, ed. M. Skov and O. Vartanian, 9–26. Amityville, NY: Baywood.
- Tatarkiewicz, W. 1970. *History of aesthetics. Vol. 1, Ancient aesthetics*. The Hague: Mouton.
- Trivers, R. L. 1971. The evolution of reciprocal altruism. *Q Rev Biol* 46:35–57.
- Tsukiura, T., and R. Cabeza. 2010. Shared brain activity for aesthetic and moral judgments: Implications for the beauty-is-good stereotype. *Soc Cogn Affect Neurosci* 6:138–48.
- Varki, A., D. H. Geschwind, and E. E. Eichler. 2008. Explaining human uniqueness: Genome interactions with environment, behaviour and culture. *Nat Rev Genet* 9:749–63.
- Vartanian, O., and V. Goel. 2004. Neuroanatomical correlates of aesthetic preference for paintings. *Neuroreport* 15:893–97.
- Veenliet, S. G., and S. V. Paunonen. 2005. Person perception based on rape-victim testimony. *Deviant Behav* 26:209–27.
- Vogt, B. A., et al. 1995. Human cingulate cortex: Surface features, flat maps, and cytoarchitecture. *J Comp Neurol* 359:490–506.
- Weeden, J., and J. Sabini. 2005. Physical attractiveness and health in Western societies: A review. *Psychol Bull* 131:635–53.
- Young, L., et al. 2007. The neural basis of the interaction between theory of mind and moral judgment. *Proc Natl Acad Sci USA* 104:8235–40.
- Zahavi, A. 1978. Decorative patterns and the evolution of art. *New Scientist* 19:182–84.
- Zaidel, D. W. 2005. *Neuropsychology of art: Neurological, cognitive, and evolutionary perspectives*. Hove, England: Psychology Press.
- Zaidel, D. W. 2010. Art and brain: Insights from neuropsychology, biology and evolution. *J Anat* 216:177–83.