



1-1-2010

# Neuroaesthetics: A coming of Age Story

Anjan Chatterjee

*University of Pennsylvania*, [anjan@mail.med.upenn.edu](mailto:anjan@mail.med.upenn.edu)

---

Suggested Citation:

Chatterjee, A. (2010). "Neuroaesthetics: A Coming of Age Story." *Journal of Cognitive Neuroscience*. Vol. 23(10). pp. 53-62.

© Massachusetts Institute of Technology

<http://www.mitpressjournals.org/loi/jocn>

This paper is posted at Scholarly Commons. [http://repository.upenn.edu/neuroethics\\_pubs/58](http://repository.upenn.edu/neuroethics_pubs/58)

For more information, please contact [repository@pobox.upenn.edu](mailto:repository@pobox.upenn.edu).

---

# Neuroaesthetics: A coming of Age Story

## **Abstract**

Neuroaesthetics is gaining momentum. At this early juncture, it is worth taking stock of where the field is and what lies ahead. Here, I review writings that fall under the rubric of neuroaesthetics. These writings include discussions of the parallel organizational principles of the brain and the intent and practices of artists, the description of informative anecdotes, and the emergence of experimental neuroaesthetics. I then suggest a few areas within neuroaesthetics that might be pursued profitably. Finally, I raise some challenges for the field. These challenges are not unique to neuroaesthetics. As neuroaesthetics comes of age, it might take advantage of the lessons learned from more mature domains of inquiry within cognitive neuroscience.

## **Disciplines**

Medicine and Health Sciences

## **Comments**

Suggested Citation:

Chatterjee, A. (2010). "Neuroaesthetics: A Coming of Age Story." *Journal of Cognitive Neuroscience*. Vol. 23(10). pp. 53-62.

© Massachusetts Institute of Technology  
<http://www.mitpressjournals.org/loi/jocn>

# Neuroaesthetics: A Coming of Age Story

Anjan Chatterjee

## Abstract

■ Neuroaesthetics is gaining momentum. At this early juncture, it is worth taking stock of where the field is and what lies ahead. Here, I review writings that fall under the rubric of neuroaesthetics. These writings include discussions of the parallel organizational principles of the brain and the intent and practices of artists, the description of informative anecdotes, and the emer-

gence of experimental neuroaesthetics. I then suggest a few areas within neuroaesthetics that might be pursued profitably. Finally, I raise some challenges for the field. These challenges are not unique to neuroaesthetics. As neuroaesthetics comes of age, it might take advantage of the lessons learned from more mature domains of inquiry within cognitive neuroscience. ■

## INTRODUCTION

What does neuroscience have to offer aesthetics? Neuroaesthetics, as a field, is gathering force (Skov & Vartanian, 2009). As it grows, the field faces the challenge of being both true to its scientific roots and relevant to aesthetics. The term *aesthetics* is used broadly to encompass the perception, production, and response to art, as well as interactions with objects and scenes that evoke an intense feeling, often of pleasure. I focus on visual aesthetics, although the principles also apply to music, dance, and literature. The term neuroaesthetics is also used broadly as a domain that has something to do with properties of the brain as it engages in aesthetics. I describe the kinds of writings that fall under the rubric of neuroaesthetics and examine what, in my view, is needed for the field to mature as a science, particularly as an experimental science. I then point to some questions worth pursuing in the near future and conclude with challenges for the field.

## NEUROAESTHETIC WRITINGS

### Parallelism

Writings on aesthetics by prominent neuroscientists highlight parallels between properties of art and organizational principles of the brain. Zeki (1999a, 1999b) should be credited for introducing neuroaesthetics into scientific discourse. He exemplifies the parallelism approach and argues forcefully that no theory of aesthetics is complete without an understanding of its neural underpinnings. He suggested that the goals of the nervous system and of artists are similar. Both are driven to understand essential visual attributes of the world. The nervous system decomposes visual information into such attributes as color, luminance, and motion. Similarly, many artists, particularly

within the last century, isolate and enhance different visual attributes. For example, Matisse emphasized color and Calder emphasized motion. Zeki suggests that artists endeavor to uncover important distinctions in the visual world and discover visual modules that are segregated functionally and anatomically within the brain.

Parallelism claims point to the fact that artists are experts of visual representations and part of their magic lies in their creative expression of this expertise. For example, Cavanagh (2005) also shows that images in paintings often violate the physics of shadows, reflections, colors, and contours. Rather than follow physical properties of the world, these painters reflect perceptual shortcuts used by our minds. Artists, in experimenting with forms of depiction, discovered what psychologists and neuroscientists are now identifying as principles of perception. Livingstone (2002) and Conway and Livingstone (2007) reveal how artists make use of complex interactions between different components of vision in creating visual effects in their paintings. Livingstone suggests that the shimmering quality of water or the sun's glow on the horizon seen in some impressionist paintings (e.g., the sun and surrounding clouds in Monet's "Impression Sunrise") is produced by isoluminant objects distinguishable only by color. This strategy plays on the distinction between the dorsal (where) and ventral (what) processing distinction (Ungerleider & Mishkin, 1982). The dorsal stream is sensitive to differences in luminance, motion, and spatial location, whereas the ventral stream is sensitive to simple form and color. Isoluminant forms are processed by the ventral stream but are not fixed with respect to motion or spatial location, as the dorsal stream does not process this information. Thus, isoluminant forms are experienced as unstable or shimmering. Conversely, because shape can be derived from luminance differences, she argues that artists can use contrast to produce shapes, and leave color for expressive, rather than descriptive, purposes. Livingstone highlights the way

---

University of Pennsylvania

that combinatorial properties of visual attributes contribute to our visual perception. Artists use these combinatorial properties to produce specific aesthetic effects.

Ramachandran and Hirstein (1999) proposed a set of perceptual principles that might underlie aesthetic experiences. They emphasize the “peak shift” phenomenon as offering insight into the aesthetics of abstract art by relying on Tinbergen’s (1954) work on this phenomenon. Tinbergen observed that sea gull chicks beg for food from their mothers by pecking on a red spot near the tip of the mother’s beak. However, the chicks respond even more vigorously to a disembodied long thin stick with three red stripes near the end. Ramachandran and Hirstein propose that neural structures that evolved to respond to specific visual stimuli respond more vigorously (a shift in their peak response) to underlying primitives of that form even when the viewer is not aware of the primitive. Their hypothesis is that artists producing abstracts make explicit use of these visual primitives in evoking aesthetic responses in viewers.

The parallelism approach to neuroaesthetics recognizes that the production and perception of art ought to conform to principles of neural organization. Properties of artworks and strategies used by artists have parallels in how the nervous system apprehends and organizes its visual world. The question for brain–art parallelism is how to translate this starting point into programmatic research with experiments testing falsifiable hypotheses.

### **Informative Anecdotes**

A good example of informative anecdotes is observations of the effects of neurological disease on the production of art (Zaidel, 2005). The effect of brain damage on the capacity to produce visual art stands in sharp contrast to its effects on many other human capacities. Diseases of the brain can impair our ability to speak or comprehend language, to coordinate movements, to recognize objects, to apprehend emotions, and to make logical decisions. Although diseases of the brain can certainly impair the ability to produce art, in some instances, paradoxically, the art seems to improve. Elsewhere, I proposed that such paradoxical improvements can be produced by a changing disposition to produce art, an enhanced visual vocabulary, better descriptive accuracy, or enhanced expressivity (Chatterjee, 2006, 2009). Here, I outline the changes in disposition and enhanced expressivity produced by these “experiments of nature.”

#### *Acquired Disposition to Produce Art*

Neurological disorders that produce obsessive–compulsive traits can also dispose people to produce art. Such a change in disposition to produce art is exemplified in a subset of patients with fronto-temporal dementias (FTDs). FTDs can cause profound changes in personality. People with FTD can be disorganized, socially disinhibited, and have

problems with their language, attention, and ability to make decisions. Despite these alterations in comportment and cognition, Miller and Hou (2004) and Miller et al. (1998) discovered that some people with FTD develop a propensity to produce art. They note that the art tends to be realistic rather than abstract or symbolic. The art is most often visual and is highly detailed. The artists with FTD themselves are intensely preoccupied with their art, suggesting that obsessive–compulsive traits acquired through their disease contributes to this artistic proclivity.

Other cases of acquired obsessive–compulsive personality traits have resulted in remarkable artistic output. Sacks (1995b) described Franco Magnani, an Italian painter in San Francisco. Magnani painted hundreds of realistic scenes of Pontito, an Italian town where he grew up. After a febrile illness, which was probably an encephalitis, he began to paint obsessively. Pontito was the only subject of his art. Sacks speculated that Magnani had partial complex seizures and was, in part, demonstrating the obsessive personality disorder sometimes associated with temporal lobe epilepsy (Waxman & Geschwind, 1975). However, instead of being hypergraphic verbally, as is more common among such people, he was hypergraphic visually. In a similar vein, Lythgoe, Polak, Kalmus, de Haan, and Khean Chong (2005) reported the case of a builder with a subarachnoid hemorrhage, who became an obsessive artist after he recovered from the initial injury. He began to draw hundreds of sketches, mostly faces. He then moved to large-scale drawings, sometimes covering entire room, and confined his art to a few themes. The authors emphasize his perseverative tendencies as critical to the emergence of his artistic skills. We also reported obsessive painting practices in an artist with Parkinson’s disease following treatment with dopamine agonists (Chatterjee, Hamilton, & Amorapanth, 2006).

A subset of autistic children produces striking visual images (Sacks, 1995a). The most detailed description of such a case was Nadia, as reported by Selfe (1977). Despite severe developmental abnormalities, Nadia had remarkable drawing skills. By the age of 3 she was drawing life-like horses. She drew intensively for a few moments at a time, always copying images. She also focused on specific kinds of images like horses, of which she drew hundreds of examples. Although Nadia’s abilities were striking, she is not unique. Autistic children with striking drawing skills seem to focus on specific subjects and draw them repeatedly.

These artists produce realistic images and tend to be preoccupied by specific themes. Although the neural basis for obsessive–compulsive disorders is not completely understood, it is associated with a dysfunction of orbito-frontal and medial-temporal cortices and fronto-striatal circuits (Kwon et al., 2003; Ursu, Stenger, Shear, Jones, & Carter, 2003; Saxena et al., 1999). Notably, in the cases described, these regions could have been damaged and posterior occipito-temporal cortices were presumably intact. The preservation of posterior cortices ensures that the neural substrates for recognizing and representing faces, places,

and objects are preserved and are thus available to be the subject of these artists' obsessions.

### *Enhanced Expressivity*

Among the most intriguing effects of brain damage on artists is the class of phenomena in which the resulting art is surprisingly appealing. Right hemisphere damage can produce left spatial neglect in which patients are unaware of the left side of space (Chatterjee, 2003). Artists with neglect omit the left side of images that they draw or paint (Blanke, Ortigue, & Landis, 2003; Cantagallo & Sala, 1998; Halligan & Marshall, 1997; Schnider, Regard, Benson, & Landis, 1993; Marsh & Philwin, 1987; Jung, 1974). As they recover from their neglect, their use of line may still be impaired. Two examples show how changed spatial representations can produce highly regarded art. Lovis Corinth, an important German artist, suffered a right hemisphere stroke in 1911. As he recovered, he resumed painting. His self portraits and portraits of his wife showed clear changes in style, with details on the left sometimes left out and textures on the left blended with the background. Alfred Kuhn characterized his later work as shifting him into the circle of great artists (quoted in Gardner, 1975). Heller (1994) reported the experience of Loring Hughes, who after a right hemisphere stroke abandoned her pre-morbid style of depictive accuracy. Instead, she turned to her own imagination and emotions. The artistic community responded well to her new images. The critic Eileen Watkins described her work as now delivering "an emotional wallop," that was not present previously.

Changes produced by left hemisphere damage are exemplified in the Bulgarian painter, Zlatio Boiyadjiev, and the Californian artist, Katherine Sherwood. Boiyadjiev's pre-morbid artistic style was natural and pictorial and he tended to use earth tones in his paintings. Following the onset of his aphasia, Boiyadjiev's paintings have been considered richer, more colorful, and containing more fluid and energetic lines (Brown, 1977; Zaimov, Kitov, & Kolev, 1969). The imagery in his work became more inventive and, at times, even bizarre and fantastical. Katherine Sherwood suffered a left hemisphere hemorrhagic stroke, which also left her with an aphasia and right-sided weakness (Waldman, 2000). Premorbidly, her images were described as "highly cerebral." After her stroke, she felt that she could not produce such images if she wanted. Her new style has been described as "raw" and "intuitive," with large irregular circular movements. She says her left hand enjoys an ease and a grace with the brush that her right hand never had, and describes it as "unburdened."

These cases are but a few examples of the neuropsychological effects of art (for comprehensive reviews, see Chatterjee, 2004b, 2009; Zaidel, 2005). The next step is to test the inferences made from these anecdotal observations. To do so, we recently developed a tool, the Assessment of Art Attributes (AAA) (Chatterjee, Widick, Sternschein, Smith, & Bromberger, 2010). The AAA can quantify

changes in specific attributes of the art of any person with brain damage. Charting such changes systematically will allow us to identify the specificity of patterns of change that happens to production of art following brain damage.

## **EXPERIMENTAL NEUROAESTHETICS**

### **Frameworks**

An experimental research program in visual neuroaesthetics rests on two principles (Chatterjee, 2002, 2004a). First, visual aesthetics, like vision in general, has multiple components. Second, aesthetic experiences emerge from a combination of responses to these different components. The process by which humans visually recognize objects offers a framework from which to consider these components. Investigations can be focused on these components and on their properties in various combinations.

The nervous system processes visual information both in hierarchical sequence and in parallel (Farah, 2000; Zeki, 1993; Van Essen, Feleman, DeYoe, Ollavaria, & Knierman, 1990). The sequential components of visual processing can be classified as early, intermediate, and late vision (Marr, 1982). Early vision extracts simple elements from the visual environment, such as color, luminance, shape, motion, and location (Livingstone & Hubel, 1987, 1988). These simple elements are processed in different parts of the brain. Intermediate vision segregates some elements and groups others together to form coherent regions in what would otherwise be a chaotic and overwhelming sensory array (Ricci, Vaishnavi, & Chatterjee, 1999; Grossberg, Mingolla, & Ros, 1997; Vecera & Behrmann, 1997; Biederman & Cooper, 1991). Late vision selects which of these coherent regions to scrutinize and evokes memories from which objects are recognized and meanings attached (Chatterjee, 2003; Farah, 2000).

The hierarchical sequence of visual processing must be reflected in visual aesthetics (Chatterjee, 2004a; for related models that also incorporate broader contextual and cultural factors, see Jacobsen, 2006; Leder, Belke, Oeberst, & Augustin, 2004). Any work of art can be decomposed into its early, intermediate, and late vision components. Aesthetic perception can distinguish between form and content (e.g., Woods, 1991; Russell & George, 1990), a distinction demonstrated experimentally (Ishai, Fairhall, & Pepperell, 2007). Similarly, scientists observe that form is processed by early and intermediate vision, whereas content is processed by later vision. Thus, the early vision features of an art object might be its color and its spatial location. These elements would be grouped together to form larger units in intermediate vision. Grouping creates "unity in diversity," a central notion of compositional balance.

Beyond perception, two other aspects of aesthetics are important. The first is the emotional response to an aesthetic image; the second is how aesthetic judgments are made. The anterior medial temporal lobe, medial

and orbito-frontal cortices, and subcortical structures mediate emotions in general, and reward systems in particular (Berridge & Kringelbach, 2008; Breiter, Aharon, Kahneman, Dale, & Shizgal, 2001; O'Doherty, Kringelbach, Rolls, Hornack, & Andrews, 2001; Delgado, Nystrom, Fissell, Noll, & Fiez, 2000; Elliott, Friston, & Dolan, 2000; Schultz, Dayans, & Montague, 1997). Aesthetic judgments about stimuli, as measured by preference ratings, are likely to engage widely distributed circuits, most importantly, dorso-lateral frontal and medial frontal cortices. The general point is that visual neuroaesthetics, like most complex biological systems, is hierarchical and can be decomposed into stable component subsystems (Simon, 1962). This hierarchical organization is precisely what makes experimental approaches to aesthetics possible.

I have emphasized a cognitive neuroscience framework for experimental neuroaesthetics. Another overarching framework to think about aesthetics comes from evolutionary theorists. They make three kinds of arguments. First, beauty serves as a proxy for health and vigor in mate selection. Second, beautiful objects are those that are complex and yet are processed efficiently. And third, art making and appreciation serves an important ritualistic function that enhances social cohesion. Space limitations do not allow an adequate consideration of evolutionary perspectives on beauty and art (see Brown & Dissanayake, 2009; Cela-Conde et al., 2009; Dissanayake, 2008; Zaidel, 2005; Grammer, Fink, Moller, & Thornhill, 2003; Penton-Voak et al., 2001; Etcoff, 1999; Rentschler, Jüttner, Unzicker, & Landis, 1999; Thornhill & Gangestad, 1999; Zahavi & Zahavi, 1997; Symons, 1979 for relevant discussions). Ultimately, evolutionary and cognitive neuroscience approaches to aesthetics are likely to converge in informative ways.

## Imaging Beauty

Beauty is central to most people's concept of aesthetics (Jacobsen, Buchta, Kohler, & Schroger, 2004). Of course, not all art is beautiful and artists do not always intend to produce beautiful things. However, beauty remains a central concept in discussions of aesthetic experiences. Understanding the neural basis of the perception of and response to beauty might give us insight into the perception of and response to visual art. Facial beauty has received most attention in cognitive neuroscience.

The response to facial beauty is likely to be deeply encoded in our biology. Cross-cultural judgments of facial beauty are quite consistent (Etcoff, 1999; Perrett, May, & Yoshikawa, 1994; Jones & Hill, 1993). Adults and children within and across cultures agree in their judgments of facial attractiveness (Langlois et al., 2000), suggesting that universal principles of facial beauty exist. Infants look longer at attractive faces within a week of being born, and the effects of facial attractiveness on infants' gaze generalize across race, sex and age by 6 months (Slater et al., 1998; Langlois, Ritter, Roggman, & Vaughn, 1991). Thus, the disposition to engage attractive faces is present in brains that

have not been modified greatly by experience. Some components of beauty are undoubtedly shaped further by cultural factors (Cunningham, Barbee, & Philhower, 2002), but the universal components are likely to have distinct neural underpinnings.

Several studies report that attractive faces activate neural circuitry involved in reward systems, including orbito-frontal cortex, the nucleus accumbens, the ventral striatum (Ishai, 2007; Kranz & Ishai, 2006; O'Doherty et al., 2003; Aharon et al., 2001; Kampe, Frith, Dolan, & Frith, 2001), and the amygdala (Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007). These regional activations are interpreted as reflecting emotional valences attached to attractive faces (Senior, 2003). The particular emotional valences are those involved in the expectation of rewards and the satisfaction of appetites. The idea that attractive faces are rewarding stimuli, at least for men, is evident behaviorally. Heterosexual men discount higher future rewards for smaller immediate rewards with attractive female faces (Wilson & Daly, 2004). Presumably, these patterns of neural activation reflect ways in which attractive faces influence mate selection (Ishai, 2007; Kranz & Ishai, 2006).

Perceptual features of faces, such as averageness, symmetry, the structure of cheekbones, the relative size of the lower half of the face, and the width of the jaw, influence people's judgments of facial beauty (Penton-Voak et al., 2001; Enquist & Arak, 1994; Grammer & Thornhill, 1994). Winston et al. (2007) found that left posterior occipito-temporal activity was enhanced by facial attractiveness.

We conducted a study to examine the extent to which facial attractiveness is apprehended automatically. Participants judged the attractiveness or matched the identity of pairs of faces. Attractiveness judgments evoked neural activity within a distributed network involving ventral visual association cortices and parts of dorsal posterior parietal and prefrontal cortices (Chatterjee, Thomas, Smith, & Aguirre, 2009). We inferred that the parietal, medial, and dorsolateral frontal activations represented neural correlates of the attention and decision-making components of this task. We also found positively correlated activity within the insula and negatively correlated activations within anterior and posterior cingulate cortex. We inferred that these patterns represent the emotional responses to attractiveness. Importantly, when subjects matched the identity of faces, attractiveness continued to evoke neural responses in ventral visual areas. This neural response was of a strength that was indistinguishable from the response when participants considered beauty explicitly. We inferred that this ventral occipital region responds to beauty automatically.

Facial attractiveness has pervasive social effects beyond its specific role in mate selection (Palermo & Rhodes, 2007; Olson & Marshuetz, 2005). Attractive individuals are considered intelligent, honest, pleasant, natural leaders (Ritts, Patterson, & Tubbs, 1992; Lerner, Lerner, Hess, & Schwab, 1991; Kenealy, Frude, & Shaw, 1988), and are

viewed as having socially desirable traits, such as strength and sensitivity (Dion, Berscheid, & Walster, 1972). The cascade of neural events that bias social decisions is likely to be triggered by an early perceptual response to attractiveness. We proposed that neural activity within ventral visual cortices in automatic response to facial attractiveness serves as the initial trigger for this cascade (Chatterjee et al., 2009).

### *Imaging Art*

A few studies have used art to examine the neural localization of aesthetic processes. Although the goals in these studies are similar, their experimental approaches differ and the results, at first glance, appear quite varied. Kawabata and Zeki (2004) asked participants to rate abstract, still life, landscape, or portrait paintings as beautiful, neutral, or ugly. Not surprisingly, they found that the pattern of activity within ventral visual cortex varied depending on whether subjects were looking at portraits, landscapes, or still lifes. In orbito-frontal (BA 11) cortex, they found greater activity for beautiful than for ugly or neutral stimuli. In anterior cingulate (BA 32) and left parietal cortex (BA39), they found greater activity for beautiful than for neutral stimuli. Only activity within orbito-frontal cortex increased with the beauty of all the painting types and the authors interpreted this activity as representing the neural underpinnings of the aesthetic emotional experience.

Vartanian and Goel (2004) used images of representational and abstract paintings in an fMRI study. They found that activity within the occipital gyri bilaterally and the left anterior cingulate increased with preference ratings. They also found that activity within the right caudate decreased as preference ratings decreased. Representational paintings evoked more activity within the occipital poles, the precuneus, and the posterior middle temporal gyrus than did abstract paintings.

Cela-Conde et al. (2004) used magnetoencephalography to record event potentials when participants viewed images of artworks and photographs. Participants judged whether or not the images were beautiful. Beautiful images evoked greater neural activity than not beautiful images over left dorsolateral prefrontal cortex with a latency of 400–1000 msec. The authors infer that this region is involved in making aesthetic judgments.

Jacobsen, Schubotz, Hofel, and von Cramon (2005) used a different strategy to investigate the neural correlates of beauty in an fMRI study. Rather than use actual artworks as their stimuli, they used a set of geometric shapes designed in the laboratory. Participants judged whether the images were beautiful or whether the images were symmetric. Participants found symmetric patterns more beautiful than nonsymmetric ones. Aesthetic judgments, more than symmetry judgments, activated medial frontal cortex (BA 9/10), the precuneus, and ventral prefrontal cortex (BA 44/47). The left intraparietal sulcus was conjointly active for symmetry and beauty judgments. Both

beauty and complexity of the images evoked activity within orbito-frontal cortex. In a follow-up study using the same stimuli (Hofel & Jacobsen, 2007), they found that beauty generated a lateral positive evoked potential in a temporal window between 360 and 1225 msec.

One might be disheartened that these studies investigating aesthetics, report inconsistent patterns of activation. Nadal, Munar, Capo, Rosselo, and Cela-Conde (2008) propose that these seemingly varied results of these studies are compatible with the general model (Chatterjee, 2004a), linking aesthetics to the neuroscience of visual and affective processing as well as reward systems and decision-making. Engaging visual properties of paintings increases activity within ventral visual cortices (Vartanian & Goel, 2004). Aesthetic judgments activate parts of dorsolateral prefrontal and medial prefrontal cortices (Jacobsen et al., 2005; Cela-Conde et al., 2004). In addition, emotional responses to these stimuli activate orbito-frontal (Jacobsen et al., 2005; Kawabata & Zeki, 2004) as well as anterior cingulate cortices (de Tommaso, Sardaro, & Livrea, 2008; Kawabata & Zeki, 2004; Vartanian & Goel, 2004).

### **FUTURE DIRECTIONS**

As neuroaesthetics moves forward, several domains could be pursued profitably. Here, I suggest three: explorations of the relationship of perception to aesthetic experiences, the nature of aesthetic judgment, and characterizing the aesthetic reward.

#### **The Relationship of Perception to Aesthetic Experiences**

As described above, visual art can be decomposed into distinct attributes such as color, line, texture, and form. Promising questions for empirical research include a better understanding of how these visual perceptual attributes contribute to the aesthetic experience. Can we measure the contributions of these attributes? Some properties of visual displays can be described with exquisite mathematical precision (Graham & Field, 2007; Redies, 2007). These quantifiable parameters might also be used in neuroscience experiments.

How much of the aesthetic experience resides in a perceptual experience and how much resides in the emotional response to artwork? Paintings of landscapes are likely to activate the parahippocampus, still lifes lateral occipital cortex, and portraits the fusiform gyrus. Does beauty modify these activations further? Perhaps these responses simply reflect category-specific activations evoked by perception itself and the aesthetic work is done within reward systems. However, many feel that we perceive beautiful objects more vividly than nonbeautiful objects. Some studies show neural responses to beauty within ventral occipito-temporal cortex. Does ventral visual cortex contain general “visual beauty detectors”? Because people are inclined to look longer at beautiful things, are such

ventral visual activations a consequence of attention or is there an independent aesthetic factor that modulates neural activity? The relationship of attention and aesthetic perception remains to be sorted out.

Fairhall and Ishai (2008), Wiesmann and Ishai (2008), and Yago and Ishai (2006) have used paintings as stimuli to study object recognition and recall. In these studies, they find activations in limbic and prefrontal regions, suggesting that emotional and reward systems are activated automatically even though participants are not making evaluations. The apparent automaticity of our response to beauty or to art is an area that invites further investigation.

One could also investigate the relationship of perception to aesthetics in brain-damaged people. Some people with brain damage probably do not perceive art in the same way that non-brain-damaged individuals do, and their emotional responses to artwork may very well differ from those of people without brain damage. Such neuropsychological investigations of aesthetic perception to date are nonexistent.

### **The Nature of Aesthetic Judgment**

Recent cognitive neuroscience methods probe individual differences. As these methods continue to develop, they could also be used to examine individual differences in aesthetic sensitivities. Aesthetic sensitivity has been referred to as a “T-factor”, for taste (Eysenck & Hawker, 1994; Eysenck, 1941). People can also develop taste with training. Behavioral studies show differences in the way that art-experienced individuals and art-naïve individuals engage with works of art (Locher, Stappers, & Overbeeke, 1999; Hekkert & Van Wieringen, 1996). Understanding the neural basis for taste and the ways aesthetic judgment might be modified with training would be of great interest.

The studies conducted thus far suggest that parts of dorsolateral and medial prefrontal cortex are involved in making aesthetic judgments. These studies do not sort out whether these brain activations are specific to aesthetic judgments or are part of neural systems that make judgments regardless of the domain under consideration. We do not know if aesthetic judgments engage neural circuits that are not engaged in other judgments.

Another issue around aesthetic judgments is the institutional context in which art is usually viewed. For example, Leder et al. (2004) argued that the same object is apprehended and evaluated differently when viewed “as artwork.” Recently, Cupchik, Vartanian, Crawley, and Mikulis (2009) showed differences in brain activations when participants looked at art paintings in an “objective and detached” manner than in a “subjective and engaged” manner with an emphasis on experiencing the mood evoked by the paintings. They found greater activity in left lateral prefrontal cortex in the latter condition, which they regard as aesthetic, than when participants looked at paintings in a detached manner. Although the cognitive mechanism underlying this difference in activation patterns is

not clear from the experiment, it demonstrates that the same object, when viewed under different conditions, can evoke different neural responses.

### **Characterizing the Aesthetic “Reward”**

Beauty is a critically important aspect of how most people think of aesthetics (Jacobsen et al., 2004). However, aesthetics is not confined to beauty. Some artwork is specifically designed to be provocative and disturbing. Ultimately, a comprehensive program in neuroaesthetics would incorporate motivations in the creation of and the response to art that engage emotional systems beyond pleasurable reward systems.

With respect to pleasure evoked by beauty or art, the imaging studies reviewed here implicate orbito-frontal cortex, the anterior and posterior cingulate, the ventral striatum including the nucleus accumbens, the caudate, and the amygdala as mediating the emotional response to beauty or to artwork. Presumably, these structures differ in their functions. We need a better sense of how the orchestration of activity within these structures contributes to an overall emotional aesthetic (Biederman & Vessel, 2006).

Evolutionary arguments for the importance of beauty often emphasize its importance in mate selection. Mate selection is a utilitarian goal and the argument is that the features that signal a desirable mate are the features we regard as beautiful. This utilitarian goal is at odds with an idea proposed in the 18th century (Kant, 1790/1987) that the aesthetic attitude is one of “disinterested interest.” On this view, aesthetic objects give pleasure without evoking additional desires. Stated differently, what distinguishes the neural response to an aesthetic experience from other rewarding experiences? Could neuroscience contribute to an understanding of disinterested interest?

Berridge and Kringelbach (2008) and Wyvell and Berridge (2000) draw a distinction between “liking” and “wanting”. Liking seems to be mediated by the nucleus accumbens shell and the ventral pallidum mediated by opioid and GABAergic neurotransmitter systems. By contrast, the mesolimbic dopaminergic system, which includes the nucleus accumbens core, might mediate wanting. Cortical structures, such as the cingulate and orbito-frontal cortex, may contribute further to conscious modulations of these liking and wanting experiences. This liking/wanting distinction is made in a rodent model with experiments using sweet and bitter tasting stimuli. Whether the liking/wanting distinction generalizes to humans or to visual stimuli remains to be seen. However, one might test the hypothesis that a self-contained reward system exists and forms the basis for aesthetic disinterested interest.

### **CHALLENGES**

These are early days in the neuroscience of visual aesthetics. With a field so young, development in any direction would be an advance. However, I suggest that practitioners



of neuroaesthetics might keep the following challenges in mind: risks of reduction, distinguishing investigations probing the brain from those probing aesthetics, and adding value to our understanding of aesthetics using neuroscience.

### **Risks of Reduction**

Experimental neuroaesthetics needs to conform to the constraints of any experimental science. That is, experiments need to be motivated by general frameworks and to test falsifiable hypotheses. Such experimental work would analyze specific components of the broader universe of aesthetics to simplify the domain needs in a way that allows experimental control. Cognitive neuroscience studies of language, emotion, and decision-making are models of this approach. Further, although qualitative analyses can certainly provide important empirical information, quantification more easily provides ways to test hypotheses rigorously.

The risk of decomposition and quantification is that reduction attenuates the very thing we are most interested in studying. Take the example of the aesthetic responses to beauty. Experimental aesthetics often addresses this issue by obtaining preference ratings from participants. One might ask methodological questions about whether forced-choice approaches or Likert-scale ratings are a more stable measure of people's preferences. One might ask whether judgments of interestingness are the same as judgments of preference. Or one might explore the relationship of complexity to either preference or to interest. These are legitimate and important questions to be pursued. However, the pursuit of such questions might easily obscure the basic question of how preference is related to aesthetic experience. Is preference a diluted version of the former? Or are deeply moving aesthetic experiences qualitatively different than those assessed in the laboratory with preference ratings? What do neuroscientists make of notions such as "the sublime?" The sublime is an emotional experience mentioned frequently in aesthetics (Kant, 1790/1987), but one that has, so far, had little traction in affective neuroscience. Reducing components of aesthetics to quantifiable measures risks inviting the proverbial problem of looking for the dropped coin under the lamp because that is where things are visible, even if the coin was dropped elsewhere. This problem is true for experimental aesthetics in general, not just neuroaesthetics.

### **Distinguishing Investigations Probing the Brain from Those Probing Aesthetics**

Art can be used to probe properties of the brain. Because brain systems devoted to aesthetics are complex and organized hierarchically, processing art potentially provides a unique window into the interactions of various subsystems. For example, abstract paintings can be used as a probe to investigate how the brain deals with indeterminate visual stimuli and tries to make sense of its visual

world (Fairhall & Ishai, 2008; Wiesmann & Ishai, 2008; Yago & Ishai, 2006). This line of work can be distinguished from those studies that use neuroscience to test hypotheses about the nature of aesthetics.

Fechner (1860), a century and a half ago, made the distinction between an outer psychophysics and an inner psychophysics. Outer psychophysics is the study of the relationship between psychology and the physical properties of stimuli. This kind of study has been the thrust of empirical aesthetics ever since. Inner psychophysics is the study of the relationship between psychology and the physical (or physiological) properties of the brain. Fechner recognized that an inner psychophysics might be possible eventually. Neuroscience technologies such as fMRI, ERPs, and transcranial magnetic stimulation now provide the means of pursuing an inner psychophysics.

The nature of the triangular relationships among psychology, outer physics, and inner physics could be made explicit. Conducting research that probes the relationship between outer and inner physics without direct recourse to psychology is possible. Here properties of objects, possibly aesthetic objects, would be/are used to probe the properties of the brain. In such experiments, finely characterized stimuli are related to the spatial and temporal response properties of neurons. Thus, one might find that the lateral occipital complex responds parametrically to some physical properties of objects, important information in its own right. The unanswered psychophysical question would be, do lateral occipital complex neurons simply serve a classification function, distinguishing between objects and other visual stimuli like faces and places, or do they also serve an evaluative function, being tuned to whether the configuration of objects are appealing as in the rich tradition of still life paintings? To answer this question, researchers would use the brain to probe the psychology of aesthetics rather than using aesthetic objects to probe properties of the brain.

A danger in experiments designed to examine the relationship between inner and outer physics is that of making inferences about the underlying psychology without adequate investigation of the relevant behavior. This general problem is recognized in cognitive neuroscience as the reverse inference problem (Poldrack, 2006), where one uses the location of neural activation to infer the underlying psychological process. Such an inference is valid as a conclusion if this area is engaged in only one psychological process. Unfortunately, such one-to-one correspondences between neural activation and psychological process are rare in the brain. Findings of localized activations to specific stimuli more often generate hypotheses about the mental processes involved, rather than confirm these hypotheses.

### **Adding Value to Our Understanding of Aesthetics Using Neuroscience**

This issue, in my view, is the most important challenge for neuroaesthetics. If the goal is to understand aesthetics (as

opposed to understanding the brain), what does neuroaesthetics offer? When does neuroscience provide deeper descriptive texture to our knowledge of aesthetics and when does it deliver added explanatory force? Knowing that the pleasure of viewing a beautiful painting is correlated with activity within orbito-frontal cortex or the nucleus accumbens adds biologic texture to our understanding of the rewards of aesthetic experiences. However, it is not obvious that it, by itself, advances our understanding of the psychological nature of that reward.

For neuroscience to make important contributions to aesthetics, the possibility of an inner psychophysics has to be taken seriously. That is, how do the physiological properties of the brain and the psychology of aesthetics relate to each other? More specifically, when does neuroscience add something to the understanding of the psychology of aesthetics that cannot be discovered by behavioral studies alone?

These are early days in neuroaesthetics. The challenges mentioned here should not be construed as causes for pessimism. These challenges apply equally to the cognitive neuroscience of any complex domain. However, as neuroaesthetics comes of age, the field can be guided by the lessons learned from investigations in more mature domains, such as the cognitive neuroscience of memory, language, and emotions.

## Acknowledgments

I thank Lisa Santer for a critical review of an early version of this article.

Reprint requests should be sent to Anjan Chatterjee, Department of Neurology and Center for Cognitive Neuroscience, 3 West Gates, 3400 Spruce Street, Philadelphia, PA 19104, or via e-mail: Anjan@mail.med.upenn.edu.

## REFERENCES

- Aharon, I., Etcoff, N., Ariely, D., Chabris, C., O'Connor, E., & Breiter, H. (2001). Beautiful faces have variable reward value: fMRI and behavioral evidence. *Neuron*, *32*, 537–551.
- Berridge, K., & Kringelbach, M. (2008). Affective neuroscience of pleasure: Reward in humans and animals. *Psychopharmacology*, *199*, 457–480.
- Biederman, I., & Cooper, E. (1991). Priming contour-deleted images: Evidence for intermediate representations in visual object recognition. *Cognitive Psychology*, *23*, 393–419.
- Biederman, I., & Vessel, E. A. (2006). Perceptual pleasure and the brain. *American Scientist*, *94*, 247–253.
- Blanke, O., Ortigue, S., & Landis, T. (2003). Color neglect in an artist. *Lancet*, *361*, 264.
- Breiter, H., Aharon, I., Kahneman, D., Dale, A., & Shizgal, P. (2001). Functional imaging of neural response to expectancy and experience of monetary gains and losses. *Neuron*, *30*, 619–639.
- Brown, J. (1977). *Mind, brain, and consciousness. The neuropsychology of cognition*. New York: Academic Press.
- Brown, S., & Dissanayake, E. (2009). The arts are more than aesthetics: Neuroaesthetics as narrow aesthetics. In M. Skov & O. Vartanian (Eds.), *Neuroaesthetics* (pp. 43–57). Amityville, NY: Baywood Publishing.
- Cantagallo, A., & Sala, S. D. (1998). Preserved insight in an artist with extrapersonal spatial neglect. *Cortex*, *34*, 163–189.
- Cavanagh, P. (2005). The artist as neuroscientist. *Nature*, *434*, 301–307.
- Cela-Conde, C. J., Ayala, F. J., Munar, E., Maestu, F., Nadal, M., Capo, M. A., et al. (2009). Sex-related similarities and differences in the neural correlates of beauty. *Proceedings of the National Academy of Sciences, U.S.A.*, *106*, 3847–3852.
- Cela-Conde, C. J., Marty, G., Maestu, F., Ortiz, T., Munar, E., Fernandez, A., et al. (2004). Activation of the prefrontal cortex in the human visual aesthetic perception. *Proceedings of the National Academy of Sciences, U.S.A.*, *101*, 6321–6325.
- Chatterjee, A. (2002). *Universal and relative aesthetics: A framework from cognitive neuroscience*. Paper presented at the International Association of Empirical Aesthetics, August 4–8, 2002, Takarazuka, Japan.
- Chatterjee, A. (2003). Neglect. A disorder of spatial attention. In M. D'Esposito (Ed.), *Neurological foundations of cognitive neuroscience* (pp. 1–26). Cambridge, MA: MIT Press.
- Chatterjee, A. (2004a). Prospects for a cognitive neuroscience of visual aesthetics. *Bulletin of Psychology and the Arts*, *4*, 55–59.
- Chatterjee, A. (2004b). The neuropsychology of visual artists. *Neuropsychologia*, *42*, 1568–1583.
- Chatterjee, A. (2006). The neuropsychology of visual art: Conferring capacity. *International Review of Neurobiology*, *74*, 39–49.
- Chatterjee, A. (2009). Prospects for a neuropsychology of art. In M. Skov & O. Vartanian (Eds.), *Neuroaesthetics* (pp. 131–143). Amityville, NY: Baywood Publishing.
- Chatterjee, A., Hamilton, R. H., & Amorapanth, P. X. (2006). Art produced by a patient with Parkinson's disease. *Behavioural Neurology*, *17*, 105–108.
- Chatterjee, A., Thomas, A., Smith, S. E., & Aguirre, G. K. (2009). The neural response to facial attractiveness. *Neuropsychology*, *23*, 135–143.
- Chatterjee, A., Widick, P., Sternschein, R., Smith, W. B., II, & Bromberger, B. (2010). The assessment of art attributes. *Empirical Studies of the Arts*, *28*, 207–222.
- Conway, B. R., & Livingstone, M. S. (2007). Perspectives on science and art. *Current Opinion in Neurobiology*, *17*, 476–482.
- Cunningham, M., Barbee, A., & Philhower, C. (2002). Dimensions of facial physical attractiveness: The intersection of biology and culture. In G. Rhodes & L. Zebrowitz (Eds.), *Facial attractiveness. Evolutionary, cognitive, and social perspectives* (pp. 193–238). Westport, CT: Ablex.
- Cupchik, G. C., Vartanian, O., Crawley, A., & Mikulis, D. J. (2009). Viewing artworks: Contributions of cognitive control and perceptual facilitation to aesthetic experience. *Brain and Cognition*, *70*, 84–91.
- de Tommaso, M., Sardaro, M., & Livrea, P. (2008). Aesthetic value of paintings affects pain thresholds. *Consciousness and Cognition*, *17*, 1152–1162.
- Delgado, M., Nystrom, L., Fissell, K., Noll, D., & Fiez, J. (2000). Tracking the hemodynamic responses for reward and punishment. *Journal of Neurophysiology*, *84*, 3072–3077.
- Dion, K., Berscheid, E., & Walster, E. (1972). What is beautiful is good. *Journal of Personality and Social Psychology*, *24*, 285–290.
- Dissanayake, E. (2008). The arts after Darwin: Does art have an origin and adaptive function? In K. Zijlemans & W. van Damme (Eds.), *World art studies: Exploring concepts and approaches* (pp. 241–263). Amsterdam: Valiz.
- Elliott, R., Friston, K., & Dolan, R. (2000). Dissociable neural responses in human reward systems. *Journal of Neuroscience*, *20*, 6159–6165.

- Enquist, M., & Arak, A. (1994). Symmetry, beauty and evolution. *Nature*, *372*, 169–172.
- Etcoff, N. (1999). *Survival of the prettiest*. New York: Anchor Books.
- Eysenck, H. J. (1941). The empirical determination of an aesthetic formula. *Psychological Review*, *48*, 83–92.
- Eysenck, H. J., & Hawker, G. W. (1994). The taxonomy of visual aesthetic preferences: An empirical study. *Empirical Studies of the Arts*, *12*, 95–101.
- Fairhall, S. L., & Ishai, A. (2008). Neural correlates of object indeterminacy in art compositions. *Consciousness and Cognition*, *17*, 923–932.
- Farah, M. (2000). *The cognitive neuroscience of vision*. Malden, MA: Blackwell Publishers.
- Fechner, G. (1860). *Elements of psychophysics* (H. Adler, Trans.). New York: Holt, Rinehart and Winston, Inc.
- Gardner, H. (1975). *The shattered mind. The person after brain damage*. New York: Alfred A. Knopf.
- Graham, D. J., & Field, D. J. (2007). Statistical regularities of art images and natural scenes: Spectra, sparseness and nonlinearities. *Spatial Vision*, *21*, 149–164.
- Grammer, K., Fink, B., Moller, A. P., & Thornhill, R. (2003). Darwinian aesthetics: Sexual selection and the biology of beauty. *Biological Review*, *78*, 385–407.
- Grammer, K., & Thornhill, R. (1994). Human (*Homo sapiens*) facial attractiveness and sexual selection: The role of symmetry and averageness. *Journal of Comparative Psychology*, *108*, 233–242.
- Grossberg, S., Mingolla, E., & Ros, W. D. (1997). Visual brain and visual perception: How does the cortex do perceptual grouping? *Trends in Neurosciences*, *20*, 106–111.
- Halligan, P. W., & Marshall, J. C. (1997). The art of visual neglect. *Lancet*, *350*, 139–140.
- Hekkert, P., & Van Wieringen, P. C. W. (1996). Beauty in the eye of expert and nonexpert beholders: A study in the appraisal of art. *American Journal of Psychology*, *109*, 389–407.
- Heller, W. (1994). Cognitive and emotional organization of the brain: Influences on the creation and perception of art. In D. Zaidel (Ed.), *Neuropsychology* (pp. 271–292). New York: Academic Press.
- Hofel, L., & Jacobsen, T. (2007). Electrophysiological indices of processing aesthetics: Spontaneous or intentional processes? *International Journal of Psychophysiology*, *65*, 20–31.
- Ishai, A. (2007). Sex, beauty and the orbitofrontal cortex. *International Journal of Psychophysiology*, *63*, 181–185.
- Ishai, A., Fairhall, S., & Pepperell, R. (2007). Perception, memory and aesthetics of indeterminate art. *Brain Research Bulletin*, *73*, 319–324.
- Jacobsen, T. (2006). Bridging the arts and sciences: A framework for the psychology of aesthetics. *Leonardo*, *39*, 155–162.
- Jacobsen, T., Bucht, K., Kohler, M., & Schroger, E. (2004). The primacy of beauty in judging the aesthetics of objects. *Psychological Reports*, *94*, 1253–1260.
- Jacobsen, T., Schubotz, R., Hofel, L., & von Cramon, D. (2005). Brain correlates of aesthetic judgments of beauty. *Neuroimage*, *29*, 276–285.
- Jones, D., & Hill, K. (1993). Criteria of facial attractiveness in five populations. *Human Nature*, *4*, 271–296.
- Jung, R. (1974). Neuropsychologie und neurophysiologie des konturund formsehens in zeichneri und malerei. In H. Weick (Ed.), *Psychopathologie Musischer Gestaltungen* (pp. 27–88). Stuttgart: FK Shattauer.
- Kampe, K., Frith, C., Dolan, R., & Frith, U. (2001). Reward value of attractiveness and gaze. *Nature*, *413*, 589.
- Kant, I. (1790/1987). *Critique of judgment* (W. S. Pluhar, Trans.). Indianapolis, IN: Hackett.
- Kawabata, H., & Zeki, S. (2004). Neural correlates of beauty. *Journal of Neurophysiology*, *91*, 1699–1705.
- Kenealy, P., Frude, N., & Shaw, W. (1988). Influence of children's physical attractiveness on teacher expectations. *Journal of Social Psychology*, *128*, 373–383.
- Kranz, F., & Ishai, A. (2006). Face perception is modulated by sexual preference. *Current Biology*, *16*, 63–68.
- Kwon, J., Kimm, J., Lee, D., Lee, J., Lee, D., Kim, M., et al. (2003). Neural correlates of clinical symptoms and cognitive dysfunctions in obsessive-compulsive disorder. *Psychiatry Research*, *122*, 37–47.
- Langlois, J., Kalakanis, L., Rubenstein, A., Larson, A., Hallam, M., & Smoot, M. (2000). Maxims or myths of beauty: A meta-analytic and theoretical review. *Psychological Bulletin*, *126*, 390–423.
- Langlois, J. H., Ritter, J. M., Roggman, L. A., & Vaughn, L. S. (1991). Facial diversity and infant preferences for attractive faces. *Developmental Psychology*, *27*, 79–84.
- Leder, H., Belke, B., Oeberst, A., & Augustin, D. (2004). A model of aesthetic appreciation and aesthetic judgments. *British Journal of Psychology*, *95*, 489–508.
- Lerner, R., Lerner, J., Hess, L., & Schwab, J. (1991). Physical attractiveness and psychosocial functioning among early adolescents. *Journal of Early Adolescence*, *11*, 300–320.
- Livingstone, M. (2002). *Vision and art: The biology of seeing*. New York: Abrams.
- Livingstone, M., & Hubel, D. (1988). Segregation of form, colour, movement, and depth: Anatomy, physiology, and perception. *Science*, *240*, 740–749.
- Livingstone, M., & Hubel, D. H. (1987). Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. *Journal of Neuroscience*, *7*, 3416–3468.
- Locher, P. J., Stappers, P. J., & Overbeeke, K. (1999). An empirical evaluation of the visual rightness theory of pictorial composition. *Acta Psychologica*, *103*, 261–280.
- Lythgoe, M., Polak, T., Kalmus, M., de Haan, M., & Khean Chong, W. (2005). Obsessive, prolific artistic output following subarachnoid hemorrhage. *Neurology*, *64*, 397–398.
- Marr, D. (1982). *Vision. A computational investigation into the human representation and processing of visual information*. New York: WH Freeman and Company.
- Marsh, G. G., & Philwin, B. (1987). Unilateral neglect and constructional apraxia in a right-handed artist with a left posterior lesion. *Cortex*, *23*, 149–155.
- Miller, B., & Hou, C. (2004). Portraits of artists: Emergence of visual creativity in dementia. *Archives of Neurology*, *61*, 842–844.
- Miller, B. L., Cummings, J., Mishkin, F., Boone, K., Prince, F., Ponton, M., et al. (1998). Emergence of artistic talent in frontotemporal dementia. *Neurology*, *51*, 978–982.
- Nadal, M., Munar, E., Capo, M. A., Rossello, J., & Cela-Conde, C. J. (2008). Towards a framework for the study of the neural correlates of aesthetic preference. *Spatial Vision*, *21*, 379–396.
- O'Doherty, J., Kringelbach, M., Rolls, E., Hornack, J., & Andrews, C. (2001). Abstract reward and punishment representations in the human orbitofrontal cortex. *Nature Neuroscience*, *4*, 95–102.
- O'Doherty, J., Winston, J., Critchley, H., Perret, D., Burt, D., & Dolan, R. (2003). Beauty in a smile: The role of orbitofrontal cortex in facial attractiveness. *Neuropsychologia*, *41*, 147–155.
- Olson, I., & Marshuetz, C. (2005). Facial attractiveness is appraised in a glance. *Emotion*, *5*, 498–502.
- Palermo, R., & Rhodes, G. (2007). Are you always on my mind? A review of how face perception and attention interact. *Neuropsychologia*, *45*, 75–92.

- Penton-Voak, I. S., Jones, B. C., Little, A. C., Baker, S., Tiddeman, B., Burt, D. M., et al. (2001). Symmetry, sexual dimorphism in facial proportions and male facial attractiveness. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, *268*, 1617–1623.
- Perrett, D. I., May, K. A., & Yoshikawa, S. (1994). Facial shape and judgements of female attractiveness. *Nature*, *368*, 239–242.
- Poldrack, R. A. (2006). Can cognitive processes be inferred from neuroimaging data? *Trends in Cognitive Sciences*, *10*, 59–63.
- Ramachandran, V. S., & Hirstein, W. (1999). The science of art: A neurological theory of aesthetic experience. *Journal of Consciousness Studies*, *6*, 15–51.
- Riedes, C. (2007). A universal model of esthetic perception based on the sensory coding of natural stimuli. *Spatial Vision*, *21*, 97–117.
- Rentschler, I., Jüttner, M., Unzicker, A., & Landis, T. (1999). Innate and learned components of human visual preference. *Current Biology*, *9*, 665–671.
- Ricci, R., Vaishnavi, S., & Chatterjee, A. (1999). A deficit of preattentive vision: Experimental observations and theoretical implications. *Neurocase*, *5*, 1–12.
- Ritts, V., Patterson, M., & Tubbs, M. (1992). Expectations, impressions, and judgments of physically attractive students: A review. *Review of Educational Research*, *62*, 413–426.
- Russell, P. A., & George, D. A. (1990). Relationships between aesthetic response scales applied to paintings. *Empirical Studies of the Arts*, *8*, 15–30.
- Sacks, O. (1995a). Prodigies. In *An anthropologist on Mars* (pp. 188–243). New York: Alfred A. Knopf.
- Sacks, O. (1995b). The landscape of his dreams. In *An anthropologist on Mars* (pp. 153–187). New York: Alfred A. Knopf.
- Saxena, S., Brody, A., Maidment, K., Dunkin, J., Colgan, M., Alborzian, S., et al. (1999). Localized orbitofrontal and subcortical metabolic changes and predictors of response to paroxetine treatment in obsessive–compulsive disorder. *Neuropsychopharmacology*, *21*, 683–693.
- Schnider, A., Regard, M., Benson, D. F., & Landis, T. (1993). Effect of a right-hemisphere stroke on an artist's performance. *Neuropsychiatry, Neuropsychology, & Behavioral Neurology*, *6*, 249–255.
- Schultz, W., Dayans, P., & Montague, P. (1997). A neural substrate of prediction and reward. *Science*, *275*, 1593–1599.
- Selfe, L. (1977). *Nadia. A case of extraordinary drawing ability in an autistic child*. New York: Academic Press.
- Senior, C. (2003). Beauty in the brain of the beholder. *Neuron*, *38*, 525–528.
- Simon, H. A. (1962). The architecture of complexity. *Proceedings of the American Philosophical Society*, *106*, 467–482.
- Skov, M., & Vartanian, O. (Eds.) (2009). *Neuroaesthetics*. Amityville, NY: Baywood Publishing.
- Slater, A., Schulenburg, C. V. D., Brown, E., Badenoch, M., Butterworth, G., Parsons, S., et al. (1998). Newborn infants prefer attractive faces. *Infant Behavior and Development*, *21*, 345–354.
- Symons, D. (1979). *The evolution of human sexuality*. Oxford, UK: Oxford University Press.
- Thornhill, R., & Gangestad, S. W. (1999). Facial attractiveness. *Trends in Cognitive Sciences*, *3*, 452–260.
- Tinbergen, N. (1954). *Curious naturalist*. New York: Basic Books.
- Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge, MA: MIT Press.
- Ursu, S., Stenger, V., Shear, M., Jones, M., & Carter, C. S. (2003). Overactive action monitoring in obsessive–compulsive disorder. *Psychological Science*, *14*, 347–353.
- Van Essen, D. C., Feleman, D. J., DeYoe, E. A., Ollavaria, J., & Knierman, J. (1990). Modular and hierarchical organization of extrastriate visual cortex in the macaque monkey. *Cold Springs Harbor Symposia on Quantitative Biology*, *55*, 679–696.
- Vartanian, O., & Goel, V. (2004). Neuroanatomical correlates of aesthetic preference for paintings. *NeuroReport*, *15*, 893–897.
- Vecera, S., & Behrmann, M. (1997). Spatial attention does not require preattentive grouping. *Neuropsychology*, *11*, 30–43.
- Waldman, P. (2000, May 12, Friday). Master stroke: A tragedy transforms a right-handed artist into a lefty and a star. *Wall Street Journal*.
- Waxman, S., & Geschwind, N. (1975). The interictal behavior syndrome associated with temporal lobe epilepsy. *Archives of General Psychiatry*, *32*, 1580–1586.
- Wiesmann, M., & Ishai, A. (2008). Recollection- and familiarity-based decisions reflect memory strength. *Frontiers in Systems Neuroscience*, *2*, 1–9.
- Wilson, M., & Daly, M. (2004). Do pretty women inspire men to discount the future. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, *271*, 177–179.
- Winston, J., O'Doherty, J., Kilner, J., Perrett, D., & Dolan, R. (2007). Brain systems for assessing facial attractiveness. *Neuropsychologia*, *45*, 195–206.
- Woods, W. A. (1991). Parameters of aesthetic objects: Applied aesthetics. *Empirical Studies of the Arts*, *9*, 105–114.
- Wyvell, C., & Berridge, K. (2000). Intra-accumbens amphetamine increases the conditioned incentive salience of sucrose reward: Enhancement of reward “wanting” without enhanced “liking” or response reinforcement. *Journal of Neuroscience*, *20*, 8122–8130.
- Yago, E., & Ishai, A. (2006). Recognition memory is modulated by visual similarity. *Neuroimage*, *31*, 807–817.
- Zahavi, A., & Zahavi, A. (1997). *The handicap principle: A missing piece of Darwin's puzzle*. Oxford, UK: Oxford University Press.
- Zaidel, D. (2005). *Neuropsychology of art*. New York: Psychology Press.
- Zaimov, K., Kitov, D., & Kolev, N. (1969). Aphasia chez un peintre. *Encephale*, *58*, 377–417.
- Zeki, S. (1993). *A vision of the brain*. Oxford, UK: Blackwell Scientific Publications.
- Zeki, S. (1999a). Art and the brain. *Journal of Consciousness Studies*, *6*, 76–96.
- Zeki, S. (1999b). *Inner vision: An exploration of art and the brain*. New York: Oxford University Press.