Review

Neuroaesthetics

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Neuroaesthetics is an emerging discipline within cognitive neuroscience that is concerned with understanding the biological bases of aesthetic experiences. These experiences involve appraisals of natural objects, artifacts, and environments. Because aesthetic encounters are common in everyday life, exploration of their biological bases can deepen our understanding of human behavior in important domains such as mate selection, consumer behavior, communication, and art. We review recent evidence showing that aesthetic experiences emerge from the interaction between sensory–motor, emotion–valuation, and meaning–knowledge neural systems. Neuroaesthetics draws from and informs traditional areas of cognitive neuroscience including perception, emotion, semantics, attention, and decision-making. The discipline is at a historical inflection point and is poised to enter the mainstream of scientific inquiry.

Introduction

Neuroaesthetics is an emerging discipline that investigates the biological underpinnings of aesthetic experiences [1–3]. Such experiences occur when we appraise objects [4]. Aesthetic experiences include emotions, valuation, and actions engendered by these objects, as well as processes that underlie their interpretation and production. Investigators typically ask how aesthetic experiences are instantiated in the brain and how knowledge of brain mechanisms informs our understanding of these experiences? The discipline merges empirical aesthetics with cognitive and affective neuroscience.

Neuroaesthetics can take a descriptive or experimental form. Descriptive neuroaesthetics relies on observations that relate facts of the brain to aesthetic experiences (Box 1). The claims are typically qualitative. Experimental neuroaesthetics, like any experimental science, produces data that are quantitative and vetted statistically. The approach tests hypotheses, predicts results, and invites replication or falsification. Humanist critics [5,6] of neuroaesthetics typically target descriptive and not experimental neuroaesthetics [7], although experimental neuroaesthetics has been criticized when concentrated too narrowly on aesthetic responses to artworks [8].

The aesthetic triad

Experiments in neuroaesthetics focus on the properties of and interactions between a triad of neural systems: sensory–motor, emotion–valuation, and meaning–knowledge circuitry (Figure 1) [9,10].

The visual brain segregates visual elements such as luminance, color, and motion, as well as higher-order objects such as faces, bodies, and landscapes. Aesthetic encounters engage these sensory systems. For example, gazing at Van Gogh's dynamic paintings evokes a subjective sense of movement and activates visual motion areas MT+ [11]. Portraits activate the face area in the fusiform gyrus (FFA) and landscape paintings activate the place area in the parahippocampal gyrus (PPA) [12,13]. Surprisingly, beyond classifying visual elements, these sensory areas may also be involved in evaluating them. Beautiful faces activate the fusiform face and adjacent areas [14]. As with faces, some studies show that neural activity in visual areas increases with the beauty of art images. The issue of how much and what kind of valuation occurs in sensory cortices is an area of active inquiry. Biederman and colleagues observed that cortical μ-opioid receptor density is greatest in parts of the ventral visual pathway that process 'stimuli that contain a great deal of interpretable information' [15]. Thus, the experience of aesthetic pleasure might arise from the interplay between brain structures that underlie perceptions of specific stimuli (e.g., PPA for scenes) and the distribution of relevant neurotransmitters in the cortex.

Looking at paintings that depict actions also engages parts of the motor system. This engagement taps into the extended mirror neuron system. Mirror neurons, first discovered in monkeys, are neurons that respond to both the execution and perception of actions [16]. A similar system exists in humans [17]. This system resonates when people infer the intent of artistic gestures or observe the consequences of actions such as in the cut canvases of Lucio Fontana. This subtle motor engagement represents an embodied element of our empathetic responses to visual art [18,19].

The pleasure that people derive from looking at beautiful objects automatically taps into our general reward circuitry [20]. For example, attractive faces activate the FFA [14] and parts of the ventral striatum [21] even when people are not thinking explicitly about the attractiveness of these faces. The orbito- and medial-frontal cortex, ventral striatum, anterior cingulate, and insula respond to beautiful visual images [22–24] and the medial orbitofrontal cortex and adjacent cingulate cortex respond to different sources of pleasures including music [25] and even architectural spaces [26].

What about meaning in art? Kirk and colleagues investigated the effects of expectations on neural responses [27].

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Box 1. Descriptive neuroaesthetics

Early neuroaesthetic writings identified parallels between the approach of artists to their visual world and brain processing of visual information. Artists at the turn of the 20th century honed in on different attributes of our visual brain [79]. For example, fauvists such as Henri Matisse and André Derain focused on color, cubists such as Pablo Picasso, George Braque, and Juan Gris focused on form, and Calder focused on visual motion [80].

Artists often depict the nature of mental representations rather than of physical objects [81]. Their renditions do not adhere strictly to the physical properties of light and shadow and color of objects. For example, they might not depict the form and contours of shadows accurately, despite the fact that they always depict shadows with less luminance than the object casting the shadow. People are insensitive to the contour but not the luminance of shadows because shadow contours are too ephemeral to provide reliable information about real world objects. Our brains never evolved to give significance to the shape of shadows.

Some artists make use of perceptual mechanisms such as the peak shift principle. This principle emerged from Tinbergen's observations of seagull chicks pecking for food from their mothers on a red spot near the tip of their mothers' beaks [82]. The chicks peck more vigorously to a disembodied long thin stick with three red stripes at the end, that is, to an exaggerated version of the inciting stimulus. Ramachandran suggested that the peak shift principle might explain the power of the exaggerated sexual dimorphic features in bronze sculptures of the 12th-century Chola dynasty in India [83]. Artists also exploit the way our visual system processes information [84] in two interacting streams [85]. Form and color are processed in one stream and tell us the 'what' of an object. Luminance, motion, and location are processed in another and tell us the 'where' of an object. The shimmering quality of water or the glow of the sun on the horizon seen in some impressionist paintings (e.g., the sun and surrounding clouds in Monet's *Impression Sunrise*) occurs because the objects are distinguished by color and not luminance. Thus, the object forms are identified but their location is hard to fix, because the 'where' stream is insensitive to boundaries and the objects appear to shimmer [86].

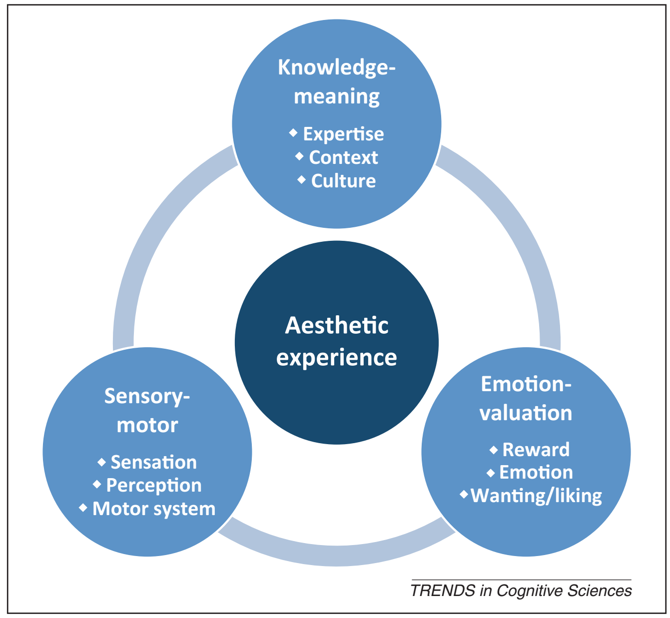

Figure 1. The aesthetic triad: neural systems contributing to emergent aesthetic experience. Aesthetic experiences are emergent states, arising from interactions between sensory–motor, emotion–valuation, and meaning–knowledge neural systems. The mechanisms by which these systems influence one another in aesthetic experiences likely mimic their interactions in other non-aesthetic engagements with objects. However, the context in which objects are encountered (e.g., as artworks) and appraisals that focus on objects rather than outcomes [40] distinguish aesthetic experiences from other evaluative encounters. This integrated view builds on earlier models that framed aesthetic experiences as the product of sequential and distinct information-processing stages, each of which isolated and analyzed a different component of an object such as an artwork [87,88]. These distinct components proved useful for laying the foundations of neuroaesthetics by mapping various aspects of information-processing stages onto specific neural structures. For example, we know that early and intermediate processing of visual aesthetics, such as processing of luminance and color and grouping, occurs in relevant parts of the occipital lobes, higher vision in the fusiform gyrus (e.g., face area in the fusiform gyrus) and medial temporal lobe (e.g., place area in the parahippocampal gyrus), and implicit actions in the motor system (e.g., mirror system). These findings confirmed the role of sensory–motor systems in automatic processing of elemental features of aesthetic objects as well as their recognition and engagement through embodied mechanisms. In addition, several regions of the emotion–valuation system of the brain contribute to aesthetic experience, including the orbitofrontal and medial frontal cortex, ventral striatum, anterior cingulate, and insula. The neural systems underlying a wide range of aesthetic emotions (e.g., awe, horror, disgust), as well as the biology of how aesthetic objects can induce moods that persist well past exposure to specific artworks, remain to be elucidated. Finally, the contribution of the meaning–knowledge system to aesthetic experience is evident from studies that manipulate the context under which stimuli are viewed, and is reflected by the modulations of activity within emotional and reward neural circuitry. Importantly, aesthetic experiences do not necessarily weigh all three systems equally. Some aesthetic phenomena can be explained without reference to emotions [89] and aesthetic responses to mathematics seem devoid of sensations [10]. Of the three systems, we know least about the contribution of the meaning–knowledge system to aesthetic experiences, partly because its manifestations are widely distributed throughout the brain and it varies substantially across individuals, cultures, and historic epochs.

People rated abstract 'art-like' images as more attractive if they were labeled as being from a museum rather than as generated by a computer. This preference was accompanied by greater neural activity in the medial orbitofrontal and ventro-medial prefrontal cortex. Thinking an image was a museum piece also produced activity in the entorhinal cortex, suggesting that people's expectations draw on memories that enhance (or probably also diminish) visual pleasure. Similarly, Lacey and colleagues found that the ventral striatum and parts of the orbitofrontal cortex were more responsive to 'art status' than to the actual content of visual images [28]. In addition, knowing the title of an artwork can facilitate greater engagement with and deepening of aesthetic experiences [29,30]. Original artworks are valued more than copies [31], consistent with our intuitive dislike for forgeries. Huang and colleagues found that people have different neural responses when told that they are looking at an authentic or copied Rembrandt portrait [32]. Authentic portraits evoked orbitofrontal activity, whereas copies evoked neural responses in the frontopolar cortex and the right precuneus. More generally, knowledge of compositional strategies, stylistic conventions, and practices can bias the attention of viewers to engage with objects aesthetically [33]. The implication of these kinds of studies is that context and knowledge beyond the sensory qualities of visual images demonstrably affects the neural responses of individuals in aesthetic experiences and may contribute to individual taste (Box 2). Recent electroencephalography (EEG) evidence suggests that such sensory and contextual integration occurs very rapidly, within 200–300 ms of seeing an artwork [34].

Beyond beauty and simple preference

Expressionist theories of art [35,36] emphasize the ability of art to communicate subtle emotions that are difficult to convey with words. Neuroaesthetic investigations of nuanced emotions beyond simple preference are beginning to surface [4,24]. For example, the 'delicate sadness' evoked by Noh masks engages the right amygdala [37]. Negative

Box 2. Individual differences in taste

Most neuroimaging studies highlight neural networks that underlie aesthetic judgments across participants rather than explore individual differences. Studies might address group differences in neural response such as those rendered by gender [90] or levels of expertise [91]. However, a focus on shared responses among viewers leaves unexplored the unique component of individual taste and its corresponding neural correlates. For example, facial attractiveness judgments between two raters correlate in the range 0.3–0.5, accounting for only 9–25% of the variance observed in ratings [92]. In fact, shared and private tastes contribute approximately equally to the variance in attractiveness ratings, where shared taste comprises all attractiveness standards that enable two judges to agree about the attractiveness of faces, and private taste comprises all attractiveness standards of a single judge that give rise to replicable disagreement with shared taste [93]. Extending this logic, individual differences in perceived facial attractiveness – measured by comparing participants who on average gave higher versus lower ratings to faces – activated the right middle temporal gyrus (MTG) exclusively [94]. Interestingly, MTG is not one of the three main cortical regions involved in face perception in humans, namely the FFA, the superior temporal sulcus, and the occipital face area [95]. Rather, MTG appears to play an important role in integrating information across modalities [96]. Its activation in relation to individual differences suggests that judgment of facial attractiveness might rely on integration of information from a variety of sources that extend beyond the domain of faces exclusively, including relevant semantic, emotional, social, and cultural factors.

People exhibit greater individual differences in their preferences for abstract art compared to preferences for real-world images [97]. Individualized profiles of ratings of 'awe' and 'pleasure' in response to paintings correlated with the degree of activation in the pontine reticular formation and the left inferior temporal sulcus, respectively [44]. Interestingly, as with facial attractiveness [94], regions of the brain that respond to individual differences in preference for paintings are dissociated from those activated by aesthetic judgment across individuals. This suggests that shared and private components of aesthetic experience can be parsed at the neural level, although the functional significance of these different neural structures remains to be worked out.

aesthetic emotions engage the lateral orbitofrontal cortex [38]. Empathetic responses to paintings engage our emotional circuitry of joy or fear or anger, mirroring the emotions expressed in artwork [18].

Eighteenth-century theoreticians, such as Kant and the Third Earl of Shaftsbury, proposed that deep aesthetic encounters are characterized by a state of disinterested interest. Such mental states occur when viewers are deeply engaged with an object without accompanying desires to acquire, control, or manipulate it. What might the correlates of disinterested interest be? Berridge and colleagues used rodent models to show that neural systems for pleasure segregate into 'liking' and 'wanting' systems [39]. Both systems typically work in concert and have overlapping neural circuitry, especially within the ventral striatum. However, the two systems are dissociable; liking is mediated by opiate and cannabinoid systems, and wanting by dopamine neurotransmitter systems. The Berridge distinction resembles that of Ortony *et al.* [40] between object-related and outcome-related emotions. In this sense, aesthetic emotions (e.g., pleasure, repulsion) are triggered by objects, in contrast to emotions triggered by outcomes (e.g., happiness, disappointment) [4]. The mental state of disinterested interest may reflect activity in the liking system without activity in the wanting system [10], with the corresponding experience of pleasurable aesthetic emotions. This hypothesis remains to be tested in humans engaged in aesthetic encounters, but might prove useful in explaining how pleasurable aesthetic responses are a subset of rewarding experiences distinct from desires for objects that drive consumer behavior.

Recently, the default mode network (DMN) has been implicated in special aesthetic states. The DMN was initially characterized as brain activity when individuals are at rest compared to periods when they perform tasks driven by external stimuli [41]. The DMN may also be active when we 'maximize the utility of moments when we are not otherwise engaged by the external world' [42,43]. Consistent with this view, the DMN is engaged when subjects explicitly focus on internal thoughts and emotions while viewing paintings [44]. Specifically, deactivation of regions that constitute the DMN – including the medial prefrontal cortex, posterior cingulate cortex, temporo–parietal junction, lateral temporal cortex, and superior frontal gyrus – was suppressed when subjects viewed paintings rated as most moving. One interpretation of this pattern of activity is that aesthetic experiences involve an internal orientation evoked by an external stimulus [45], a mental signature of deeply aesthetic moments. Consistent with the notion that aesthetic experiences include an important internally oriented component, subjects focusing on the feelings that artworks evoke exhibit bilateral activation of the insulae [46], regions strongly implicated in regulating our autonomic nervous system and the visceral experience of emotions [47].

Using magnetoencephalography (MEG), Cela-Conde and colleagues proposed that aesthetic responses occur at two levels [48]. MEG assesses neural responses with a temporal fidelity not possible with functional MRI. The authors found that different neural patterns were evoked following an initial exposure to artwork, one within 250 ms and one between 1000 and 1500 ms. The later, but not the earlier, response is tethered to the DMN. This effect can be interpreted using the appraisal theory of emotions [49], according to which subjective goals and desires influence emotional reactions to objects and events in the world. The delayed MEG response found by Cela-Conde and colleagues may reflect the effects of cognitive appraisals on emotional experiences with artworks. This theory is directly relevant to aesthetic encounters more generally [50] and explains why the same painting can evoke anger in one person, curiosity in another, and amusement in a third.

The paradoxical facilitation of art

Patient observations are an important source of data in neuroaesthetics [51–54] especially with regard to artistic production, processes that are not easily studied using imaging (Box 3). Paradoxically, neurological disease sometimes improves artistic production.

Frontotemporal dementias (FTD) are a group of degenerative neurological diseases that can profoundly change the personality of affected individuals. Such people often become disinhibited and disorganized, and have problems with language, attention, and the ability to make decisions. A few individuals with FTD develop a propensity to produce art. Their art is typically realistic, obsessive, and

Box 3. Aesthetics and hemispheric laterality

The popular notion that the right hemisphere is the artistic hemisphere is likely wrong. According to this view, damage to the right hemisphere should profoundly affect artistic production and left hemisphere damage should largely spare such abilities. The Assessment of Art Attributes (AAA) is a tool that quantitatively assesses attributes applicable to visual artwork [98]. These attributes refer to the form (balance, color saturation, color temperature, depth, complexity, and stroke style) and content (abstractness, animacy, emotionality, realism, representational accuracy, and symbolism) of artwork. The AAA was used to assess changes in the artwork of three patients with lateralized brain damage; Sherwood and Boiyadjiev both had left brain damage, and Corinth had right brain damage [99]. The assessment showed that brain damage does not result in a prototypic style of painting. Rather, brain damage might produce a prototypic shift in painting style. The artistic styles of Sherwood and Boiyadjiev are very different from each other. For example, Sherwood's paintings started out substantially flatter than those of Boiyadjiev. Yet the paintings of both artists became flatter following their strokes, despite the fact that in terms of flatness, Sherwood's paintings before her stroke were more similar to Boiyadjiev's paintings after his stroke. The paintings of all three artists became more abstract and distorted and less realistic and accurate. They were also rendered with looser strokes, greater flatness, and vibrance. Thus, none of these changes can be ascribed to laterality of brain functions. All the changes observed in Corinth's paintings were also observed in those of Sherwood and Boiadjiev. Both hemispheres participate in artistic production because the art created by these artists changed regardless of which hemisphere was damaged. If anything, damage to the left hemisphere induced more extensive alterations in artistic production, including in the symbolism depicted, than did damage to the right hemisphere.

detailed [55]. This artistic output is a consequence of acquired obsessive–compulsive traits that are expressed graphically. Other clinical examples, including artistic savants with autism, confirm that obsessive–compulsive traits can predispose individuals to produce art [56–59]. Obsessive–compulsive traits imply dysfunction of the orbitofrontal and medial temporal cortices and fronto–striatal circuits [60]. Notably, the posterior occipito–temporal cortices remain intact. Preservation of the posterior cortices ensures that the neural substrates representing faces, places, and objects are preserved and are available as the object of these patients' obsessions.

Right hemisphere damage can produce left spatial neglect and artists with neglect omit the left side of images that they produce. Lovis Corinth, an important German artist, left out details and textures on the left of his portraits after suffering a right hemisphere stroke in 1911. These works were regarded highly by critics [61]. Loring Hughes was an artist who had difficulty in coordinating the spatial relationship between lines after a right hemisphere stroke. This forced her to abandon her premorbid style of realistic depictions. Instead she relied on her own imagination and emotions for inspiration [62]. Artists with left brain damage sometimes introduce more vivid colors and change the content of their imagery. The premorbid artistic style of Bulgarian painter Zlatio Boiadjiev was natural and pictorial and he used earth tones. Following his stroke, Boiadjiev's paintings were richer and more colorful, fluid, energetic, and even fantastical [63,64]. The Californian artist Katherine Sherwood suffered a left hemisphere stroke. Premorbidly, her images were 'highly cerebral', incorporating esoteric images of cross-dressers, medieval seals, and spy photos. After her stroke, Sherwood described her new style as 'raw' and 'intuitive', and her left hand as 'unburdened', enjoying an ease and grace with the brush that her right hand never had [65].

A few artists with Alzheimer's disease continue to paint after the onset of their illness [66–69]. William Utermohlen painted several self-portraits during the course of his illness. These increasingly simplified and distorted portraits became haunting psychological self-expressions. Willem de Kooning is the best-known artist who continued to paint after the onset of Alzheimer's disease. Some experts regard this late period as representing a new and coherent style, with distillation of forms from earlier works into their essence [70].

The observation that art can improve after neurological disease demonstrates that the brain does not harbor a single art module. The final artistic output emerges from coordination of different components organized in a flexible ensemble across the brain. Brain damage alters the available components such that art is produced using a different set of components within this ensemble. This neural system is like a hanging mobile. The mobile rests in equilibrium established by its weighted components. If a particular component is removed, the entire configuration might collapse or it might find a new resting state that differs from the original but is nevertheless appealing. Similarly, brain damage might render an artist incapable of working, analogous to collapse of the mobile, or the individual might settle into a new equilibrium in which art emerges in new and interesting configurations.

Noninvasive brain stimulation methods use magnetic pulses or direct electrical currents to produce virtual lesions or enhancements to specific parts of the brain. Such methods can test the hypothesis that flexible neural ensembles underpin aesthetic experiences by examining how changes in neural activity in local areas modulate aesthetic experiences. For example, stimulation of the left dorsolateral prefrontal cortex makes individuals like representational paintings more than they do under sham stimulation conditions [71].

Limitations

Are there principled limits to neuroscientific contributions to aesthetics? The role of meaning in aesthetic experiences might be such a limit. Current neuroscientific methods are adept at investigating stable and relatively universal properties of the mind (Box 3). We apprehend the general meaning of a scene quickly. In the same way that we easily interpret objects seen through the frame of a window, we easily interpret objects seen in the frame of representational artwork. The ability to quickly grasp the meaning of objects might contribute to why viewers prefer representational over abstract paintings [72] (although expertise in the visual arts attenuates this difference [73]). Studies that use artwork with ambiguous objects capitalize on the ease with which people recognize objects and show that the neural response to such images is more likely to engage structures involved in imagery [74].

Beyond conveying the general semantics of recognizable objects, artworks are often vehicles for culturally

Box 4. Outstanding questions

- Is the valuation of aesthetic objects computed in sensory cortices?
- What is the relationship between aesthetic judgments and approach–avoidance responses?
- Do different parts of the extended reward circuitry play different roles in aesthetic rewards?
- How are different aesthetic emotions, including negative ones such as horror and disgust, implemented in the brain and how do these emotions give us pleasure?
- How do aesthetic objects evoke moods in viewers that persist after an encounter with an artwork?
- What exactly is the role of the DMN in aesthetic experiences?
- What unique contribution, if any, does each hemisphere make to aesthetic perception and production?
- Are there gender differences in aesthetic experiences?
- How does expertise in the visual arts alter neural structures and functional responses to aesthetic objects?
- Do brain regions that compute aesthetic judgments overlap with regions that compute other socially and culturally relevant values such as morality and justice?
- What are the evolutionary underpinnings of the ability of the brain to experience aesthetic pleasure?
- How can art perception and creation be used therapeutically?

contingent ideas. The meaning of individual works of art is fluid and subject to different interpretations across people and historical epochs [75]. Reaction to art, whether joy or disgust or anger, is often a reaction to the ideas being conveyed [76]. An understanding of the historical context in which a work is produced, the intent of the artist, the potential meanings that it conveys, and the social and cultural conversation in which it is engaged enhances the appreciation of the artwork [77]. Neuroscience methods do not easily address this level of textured meaning embedded within individual works of art [10].

Concluding remarks

These are early days in neuroaesthetics [1,2]. The contours of the field and its methods and research agenda are evolving. The domain cuts across traditional areas of cognitive neuroscience such as perception, emotion, semantics, attention, and decision-making. Scientists who typically work in these traditional areas could easily add neuroaesthetics to their catalog of concerns. The biggest challenge for neuroaestheticians is to get past the inference of psychological mechanisms based solely on the location of neural activity. Such reverse inferences [78] are better framed for the generation of hypotheses rather than confirming them. Technical advances in neuroscience methods will continue to offer new experimental assays to test these hypotheses and engagement with humanists will deepen the very hypotheses under consideration (Box 4). The discipline is at a historical inflection point and is poised to enter the mainstream of scientific inquiry.

References

1 Skov, M. and Vartanian, O., eds (2009) *Neuroaesthetics*, Baywood Publishing Company
2 Chatterjee, A. (2011) Neuroaesthetics: a coming of age story. *J. Cogn. Neurosci.* 23, 53–62
3 Nadal, M. and Pearce, M.T. (2011) The Copenhagen Neuroaesthetics Conference: prospects and pitfalls for an emerging field. *Brain Cogn.* 76, 172–183
4 Brown, S. *et al.* (2011) Naturalizing aesthetics: brain areas for aesthetic appraisal across sensory modalities. *Neuroimage* 58, 250–258
5 Croft, J. (2011) The challenges of interdisciplinary epistemology in neuroaesthetics. *Mind Brain Educ.* 5, 5–11
6 Tallis, R. (2008) The limitations of a neurological approach to art. *Lancet* 372, 19–20
7 Chatterjee, A. (2011) Where there be dragons: finding the edges of neuroaesthetics. *Am. Soc. Neuroaesth. Newsl.* 31, 4–6
8 Brown, S. and Dissanayake, E. (2009) The arts are more than aesthetics: neuroaesthetics as narrow aesthetics. In *Neuroaesthetics* (Skov, M. and Vartanian, O., eds), pp. 43–57, Baywood Publishing Company
9 Shimamura, A.P. (2012) Towards a science of aesthetics. In *Aesthetic Science: Connecting Minds, Brains and Experience* (Shimamura, A.P. and Palmer, S.E., eds), pp. 3–28, Oxford University Press
10 Chatterjee, A. (2014) *The Aesthetic Brain: How We Evolved to Desire Beauty and Enjoy Art*, Oxford University Press
11 Thakral, P.P. *et al.* (2012) A neural mechanism for aesthetic experience. *Neuroreport* 23, 310–313
12 Kawabata, H. and Zeki, S. (2004) Neural correlates of beauty. *J. Neurophysiol.* 91, 1699–1705
13 Yue, X. *et al.* (2007) The neural basis of scene preferences. *Neuroreport* 18, 525–529
14 Chatterjee, A. *et al.* (2009) The neural response to facial attractiveness. *Neuropsychology* 23, 135–143
15 Biederman, I. and Vessel, E.A. (2006) Perceptual pleasure and the brain. *Am. Sci.* 94, 247–253
16 Gallese, V. *et al.* (1996) Action recognition in the premotor cortex. *Brain* 119, 593–609
17 Cattaneo, L. and Rizzolatti, G. (2009) The mirror neuron system. *Arch. Neurol.* 66, 557–560
18 Freedberg, D. and Gallese, V. (2007) Motion, emotion and empathy in esthetic experience. *Trends Cogn. Sci.* 11, 197–203
19 Umilta, M.A. *et al.* (2012) Abstract art and cortical motor activation: an EEG study. *Front. Hum. Neurosci.* 6, 311
20 Kühn, S. and Gallinat, J. (2012) The neural correlates of subjective pleasantness. *Neuroimage* 61, 289–294
21 Kim, H. *et al.* (2007) Temporal isolation of neural processes underlying face preference decisions. *Proc. Natl. Acad. Sci. U.S.A.* 104, 18253–18258
22 Vartanian, O. and Goel, V. (2004) Neuroanatomical correlates of aesthetic preference for paintings. *Neuroreport* 15, 893–897
23 Jacobsen, T. *et al.* (2005) Brain correlates of aesthetic judgments of beauty. *Neuroimage* 29, 276–285
24 Jacobs, R.H.A.H. *et al.* (2012) Neural correlates of visual aesthetics – beauty as the coalescence of stimulus and internal state. *PLoS ONE* 7, e31248
25 Ishizu, T. and Zeki, S. (2011) Toward a brain-based theory of beauty. *PLoS ONE* 6, e21852
26 Vartanian, O. *et al.* (2013) Impact of contour on aesthetic judgments and approach–avoidance decisions in architecture. *Proc. Natl. Acad. Sci. U.S.A.* 110, 10446–10453
27 Kirk, U. *et al.* (2009) Modulation of aesthetic value by semantic context: an fMRI study. *Neuroimage* 44, 1125–1132
28 Lacey, S. *et al.* (2011) Art for reward's sake: visual art recruits the ventral striatum. *Neuroimage* 55, 420–433
29 Leder, H. *et al.* (2006) Entitling art: influence of title information on understanding and appreciation of paintings. *Acta Psychol. (Amst.)* 121, 176–198
30 Millis, K. (2001) Making meaning brings pleasure: the influence of titles on aesthetic experiences. *Emotion* 1, 320–329
31 Newman, G.E. and Bloom, P. (2012) Art and authenticity: the importance of originals in judgments of value. *J. Exp. Psychol. Gen.* 141, 558–569
32 Huang, M. *et al.* (2011) Human cortical activity evoked by the assignment of authenticity when viewing works of art. *Front. Hum. Neurosci.* 5, 134
33 Seeley, W.P. (2013) Art, meaning, and perception: a question of methods for a cognitive neuroscience of art. *Br. J. Aesth.* 53, 443–460
34 Noguchi, Y. and Murota, M. (2013) Temporal dynamics of neural activity in an integration of visual and contextual information in an esthetic preference task. *Neuropsychologia* 51, 1077–1084
35 Tolstoy, L. (1899) *What is Art*, Crowell & Co

36 Collingwood, R.G. (1958) *The Principles of Art*, Oxford University Press
37 Osaka, N. *et al.* (2012) Neural correlates of delicate sadness: an fMRI study based on the neuroaesthetics of Noh masks. *Neuroreport* 23, 26–29
38 Munar, E. *et al.* (2012) Lateral orbitofrontal cortex involvement in initial negative aesthetic impression formation. *PLoS ONE* 7, e38152
39 Berridge, K.C. *et al.* (2009) Dissecting components of reward: 'liking', 'wanting', and learning. *Curr. Opin. Pharmacol.* 9, 65–73
40 Ortony, A. *et al.* (1988) *The Cognitive Structure of Emotions*, Cambridge University Press
41 Raichle, M.E. *et al.* (2001) A default mode of brain function. *Proc. Natl. Acad. Sci. U.S.A.* 98, 676–682
42 Buckner, R.L. *et al.* (2008) The brain's default network. *Ann. N. Y. Acad. Sci.* 1124, 1–38
43 Christoff, K. *et al.* (2009) Experience sampling during fMRI reveals default network and executive system contributions to mind wandering. *Proc. Natl. Acad. Sci. U.S.A.* 106, 8719–8724
44 Vessel, E.A. *et al.* (2012) The brain on art: intense aesthetic experience activates the default mode network. *Front. Hum. Neurosci.* 6, 66
45 Vessel, E.A. *et al.* (2013) Art reaches within: aesthetic experience, the self and the default mode network. *Front. Neurosci.* 7, 258
46 Cupchik, G.C. *et al.* (2009) Viewing artworks: contributions of cognitive control and perceptual facilitation to aesthetic experience. *Brain Cogn.* 70, 84–91
47 Critchley, H.D. *et al.* (2005) Activity in the human brain predicting differential heart rate responses to emotional facial expressions. *Neuroimage* 24, 751–762
48 Cela-Conde, C.J. *et al.* (2013) Dynamics of brain networks in the aesthetic appreciation. *Proc. Natl. Acad. Sci. U.S.A.* 110 (Suppl. 2), 10454–10461
49 Roseman, I.J. and Smith, C.A. (2001) Appraisal theory: overview, assumptions, varieties, controversies. In *Appraisal Processes in Emotion: Theory, Methods, Research* (Klaus, S.R. *et al.*, eds), pp. 3–19, Oxford University Press
50 Sylvia, P.J. (2012) Human emotions and aesthetic experience. In *Aesthetic Science: Connecting Minds, Brains, and Experience* (Shimamura, A. and Palmer, S., eds), pp. 250–275, Oxford University Press
51 Chatterjee, A. (2004) The neuropsychology of visual artists. *Neuropsychologia* 42, 1568–1583
52 Chatterjee, A. (2009) Prospects for a neuropsychology of art. In *Neuroaesthetics* (Skov, M. and Vartanian, O., eds), pp. 131–143, Baywood Publishing Company
53 Zaidel, D. (2005) *Neuropsychology of Art*, Psychology Press
54 Bogousslavsky, J. and Boller, F. (2005) *Neurological Disorders in Famous Artists*, Karger
55 Miller, B.L. *et al.* (1998) Emergence of artistic talent in frontotemporal dementia. *Neurology* 51, 978–982
56 Sacks, O. (1995) The landscape of his dreams. In *An Anthropologist on Mars*. pp. 153–187, Alfred A. Knopf
57 Lythgoe, M. *et al.* (2005) Obsessive, prolific artistic output following subarachnoid hemorrhage. *Neurology* 64, 397–398
58 Chatterjee, A. (2006) The neuropsychology of visual art: conferring capacity. *Int. Rev. Neurobiol.* 74, 39–49
59 Selfe, L. (1977) *Nadia. A Case of Extraordinary Drawing Ability in an Autistic Child*, Academic Press
60 Kwon, J. *et al.* (2003) Neural correlates of clinical symptoms and cognitive dysfunctions in obsessive-compulsive disorder. *Psychiatry Res.* 122, 37–47
61 Gardner, H. (1975) *The Shattered Mind. The Person After Brain Damage*, Alfred A. Knopf
62 Heller, W. (1994) Cognitive and emotional organization of the brain: influences on the creation and perception of art. In *Neuropsychology* (In: Zaidel, D., ed.), pp. 271–292, Academic Press
63 Zaimov, K. *et al.* (1969) Aphasie chez un peintre. *Encephale* 58, 377–417
64 Brown, J. (1977) *Mind, Brain, and Consciousness. The Neuropsychology of Cognition*, Academic Press
65 Sherwood, K. (2012) How a cerebral hemorrhage altered my art. *Front. Hum. Neurosci.* 6, 55
66 Miller, B. and Hou, C. (2004) Portraits of artists: Emergence of visual creativity in dementia. *Arch. Neurol.* 61, 842–844
67 Maurer, K. and Prvulovic, D. (2004) Paintings of an artist with Alzheimer's disease: visuoconstructive deficits during dementia. *J. Neural Transm.* 111, 235–245
68 Crutch, S. *et al.* (2001) Some workmen can blame their tools: artistic change in an individual with Alzheimer's disease. *Lancet* 347, 1096–1098
69 van Buren, B. *et al.* (2013) Changes in painting styles of two artists with Alzheimer's disease. *Psychol. Aesth. Creativity Arts* 7, 89–94
70 Garrels, G. (1995) Three toads in the garden: line, color, and form. In *Willem de Kooning. The Late Paintings, The 1980s*. pp. 9–37, San Francisco Museum of Modern Art and Walker Arts Center
71 Cattaneo, Z. *et al.* (2013) The world can look better: enhancing beauty experience with brain stimulation. *Soc. Cogn. Affect. Neurosci.* http://dx.doi.org/10.1093/scan/nst165
72 Leder, H. *et al.* (2012) How art is appreciated. *Psychol. Aesth. Creativity Arts* 6, 2–10
73 Hekkert, P. and van Wieringen, P.C.W. (1996) The impact of level of expertise on the evaluation of original and altered versions of post-impressionistic paintings. *Acta Psychol.* 94, 117–131
74 Fairhall, S.L. and Ishai, A. (2008) Neural correlates of object indeterminacy in art compositions. *Conscious. Cogn.* 17, 923–932
75 Bullot, N.J. and Reber, R. (2013) The artful mind meets art history: toward a psycho-historical framework for the science of art appreciation. *Behav. Brain Sci.* 36, 123–137
76 Gopnik, B. (2012) Aesthetic science and artistic knowledge. In *Aesthetic Science: Connecting Minds, Brains and Experience* (Shimamura, A.P. and Palmer, S.E., eds), pp. 129–159, Oxford University Press
77 Tinio, P.P.L. (2013) From artistic creation to aesthetic reception: the mirror model of art. *Psychol. Aesth. Creativity Arts* 7, 265–275
78 Poldrack, R. (2006) Can cognitive processes be inferred from neuroimaging data? *Trends Cogn. Sci.* 10, 59–63
79 Zeki, S. (1999) Art and the brain. *J. Conscious. Stud.* 6, 76–96
80 Zeki, S. and Lamb, M. (1994) The neurology of kinetic art. *Brain* 117, 607–636
81 Cavanagh, P. (2005) The artist as neuroscientist. *Nature* 434, 301–307
82 Tinbergen, N. (1954) *Curious Naturalist*, Basic Books
83 Ramachandran, V.S. and Hirstein, H. (1999) The science of art: a neurological theory of aesthetic experience. *J. Conscious. Stud.* 6, 15–51
84 Conway, B.R. and Livingstone, M.S. (2007) Perspectives on science and art. *Curr. Opin. Neurobiol.* 17, 476–482
85 Ungerleider, L.G. and Mishkin, M. (1982) Two cortical visual systems. In *Analysis of Visual Behavior* (Ingle, D.J. *et al.*, eds), pp. 549–586, MIT Press
86 Livingstone, M. (2002) *Vision and Art: The Biology of Seeing*, Abrams
87 Chatterjee, A. (2004) Prospects for a cognitive neuroscience of visual aesthetics. *Bull. Psychol. Arts* 4, 55–59
88 Leder, H. *et al.* (2004) A model of aesthetic appreciation and aesthetic judgments. *Br. J. Psychol.* 95, 489–508
89 Martindale, C. (2001) How does the brain compute aesthetic experience? *Gen. Psychol.* 36, 25–35
90 Cela-Conde, C.J. *et al.* (2009) Sex-related similarities and differences in the neural correlates of beauty. *Proc. Natl. Acad. Sci. U.S.A.* 106, 3847–3852
91 Kirk, U. *et al.* (2009) Brain correlates of aesthetic expertise: a parametric fMRI study. *Brain Cogn.* 69, 306–315
92 Thornhill, R. and Gangestad, S.W. (1999) Facial attractiveness. *Trends Cogn. Sci.* 3, 452–460
93 Hönekopp, J. (2006) Once more: is beauty in the eye of the beholder? Relative contributions of private and shared taste to judgments of facial attractiveness. *J. Exp. Psychol. Hum. Percept. Perform.* 32, 199–209
94 Vartanian, O. *et al.* (2013) Middle temporal gyrus encodes individual differences in perceived facial attractiveness. *Psychol. Aesth. Creativity Arts* 7, 38–47
95 Kanwisher, N. and Yovel, G. (2009) Cortical specialization for face perception in humans. In *Handbook of Neuroscience for the Behavioral Sciences* (Cacioppo, J.T. and Bernston, G.G., eds), pp. 841–858, Wiley and Sons
96 Weiner, K. and Grill-Spector, K. (2013) Neural representations of faces and limbs neighbor in human high-level visual cortex: evidence for a new organization principle. *Psychol. Res.* 77, 74–97
97 Vessel, E.A. and Rubin, N. (2010) Beauty and the beholder: highly individual taste for abstract, but not real-world images. *J. Vis.* 10, 18
98 Chatterjee, A. *et al.* (2010) The assessment of art attributes. *Emp. Stud. Arts* 28, 207–222
99 Chatterjee, A. *et al.* (2011) Artistic production following brain damage: a study of three artists. *Leonardo* 44, 405–410