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Neuroscience of aesthetics

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Aesthetic evaluations are appraisals that influence choices in important domains of human activity, including mate selection, consumer behavior, art appreciation, and possibly even moral judgment. The nascent field of *neuroaesthetics* is advancing our understanding of the role of aesthetic evaluations by examining their biological bases. Here, we conduct a selective review of the literature on neuroaesthetics to demonstrate that aesthetic experiences likely emerge from the interaction between emotion–valuation, sensory–motor, and meaning–knowledge neural systems. This tripartite model can in turn be evoked to explain phenomena central to aesthetics, such as context effects on preferences. Indeed, context-dependent appraisals that focus on objects rather than on outcomes could be an important factor distinguishing aesthetic experiences from other kinds of evaluations.

Keywords: art; aesthetics; beauty; context; preference

Introduction

The effects of aesthetic judgments—broadly defined as evaluative appraisals of objects—are pervasive and profound in our lives. Take physical attractiveness, for example. Facial beauty is an important factor in partner selection.[1] In fact, the positive effects of physical attractiveness extend to assessments of even seemingly unrelated characteristics, such as personality, marital satisfaction, employment success, and moral goodness.[2–4] Similar aesthetic effects are observed in consumer choice. For example, the beauty assigned to a physical space is the most important factor driving one's desire to live in that space,[5] validating widespread attention given to design aesthetics in contemporary culture. Then, there are the well-established aesthetic effects underlying art appreciation, experienced by museumgoers the world over. For example, approximately five million people visit the Metropolitan Museum of Art in New York City each year,[6] attesting to the allure that art has for people. Importantly, aesthetic effects extend beyond mere appreciation of art to our willingness to purchase art—not an insignificant consideration, given that annual global art auction revenues surpassed $11.5 billion in 2011.[7]

Despite notable differences in features across these various domains of human activity, we argue that, at their core, aesthetic experiences are underpinned by a limited set of shared neural systems: the emotion–valuation, sensory–motor, and meaning–knowledge systems.[8] This view has arisen on the basis of the available empirical evidence in the nascent field of *neuroaesthetics*, an emerging discipline within cognitive neuroscience focused on understanding the biological bases of aesthetic experiences.[9–12] Specifically, the aesthetic evaluation of cultural artifacts (e.g., paintings, architecture, sculpture, music) activates the same neural systems that are activated while evaluating primary reinforcers (e.g., food, drink), giving rise to the notion of a "common currency" for choice that transcends domains.[13] However, to fully appreciate the *raison d'être* of neuroaesthetics, it is necessary to first take a historical journey back to the origins of psychological aesthetics, the second oldest discipline in experimental psychology.

Historical origins of neuroaesthetics

The publication of Gustav Theodor Fechner's *Vorschule der Aesthetik* in 1876 marks the beginning

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of psychological aesthetics.[14,15] As a psychophysicist, Fechner worked under the assumption that a correspondence exists between the physical properties of stimuli and the sensations that they cause. It is important to emphasize that, in Fechner's time, it was not possible to directly observe neural processes that mediate the relationship between physical properties of stimuli and their psychological consequences (e.g., sensations). Nevertheless, cognizant of the role that they play in the mechanisms he was trying to unearth, Fechner distinguished between *outer* and *inner psychophysics*: whereas outer psychophysics involves the relationship between variations in the physical properties of stimuli and the sensations that they cause, inner psychophysics involves the relationship between those sensations and the neural activities that underlie them. In this sense, Fechner was truly ahead of his time in anticipating one of the main goals of modern neuroscience, which involves establishing correspondences between neural and mental processes.[16,17]

Recent advances in cognitive neuroscience have made it possible to realize the full spectrum of research possibilities that Fechner envisioned well over a century ago. Here, it is important to emphasize that the aim of neuroaesthetics is not to reduce aesthetic experience to its biological bases. Rather, the pursuit is motivated by an appreciation of Aristotle's classic framework for understanding the causes of human behavior. Specifically, Aristotle argued that to fully understand the causal structure of any phenomenon it is necessary to understand it along four different strands.[18,19] Understanding a phenomenon's *efficient* causes means understanding the triggers that generate or prevent its effect from occurring. For example, does the mere presentation of a face trigger an aesthetic evaluation? Understanding its *final* causes involves functional explanations that address purposive questions, such as what the effect is supposed to accomplish. *Formal* causes are models that specify the transition from efficient causes to final causes (i.e., the system of relationships). Finally, *material* causes are explanations of the substrates that give rise to it. Although, by virtue of its focus on the biological bases of aesthetic experiences, neuroaesthetics is concerned with material causes, our review will demonstrate that its purview extends to all four causes in an effort to build a more complete understanding of aesthetic experiences.[12]

Fechner's ideas continue to exert a strong influence on research in empirical aesthetics today, including neuroaesthetics.[15,17] These influences are most strongly exhibited by two prevalent research trends. First, Fechner advocated strongly for an experimental aesthetics "from below," suggesting that one's focus should be on studying the effects of stimulus-driven bottom-up processes on sensation, perception, and judgment. This trend is reflected in the designs of many contemporary studies wherein specific stimulus features are manipulated systematically to quantify their effects on aesthetic experiences. Second, since Fechner, there has been a push by major thinkers in the field to discover a finite set of universal laws that govern people's aesthetic interactions with objects.[20,21] Recently, however, both of these historical trends have been extended by researchers who increasingly focus on quantifying the effects of contextual and historical influences on aesthetic experiences.[22] In addition, both of these trends are reflected in the pioneering work of Semir Zeki, credited for introducing the term "neuroaesthetics" into scientific discourse.[23,24]

Because a significant portion of the evidential base for neuroaesthetics has emerged from brain imaging studies—in particular functional magnetic resonance imaging (fMRI)—it is important to highlight some of the basic limitations of this approach. First and foremost, by and large neuroimaging techniques generate correlational data. As such, when used in isolation, they do not allow one to make causal inferences about neural function. To do so, it is necessary to triangulate findings across multiple methodological approaches, including behavioral, electrophysiological, and lesion studies.[25] Second, fMRI is a measure of neuronal mass activity, making inferences about the involvement of specific processes driven by specific classes of neurons problematic.[26] Finally, many of the neuroimaging studies to date have relied on the analytic method of subtractive contrasts, meaning that the activations reveal relative rather than absolute differences in relation to experimental manipulations. This is not necessarily a shortcoming if the research question involves testing for relative differences, but it does become an issue if the presence versus absence of a process must be inferred.[27] Indeed, researchers have recently relied on increasingly fine-tuned analytic techniques for making inferences about mental processes.[28,29] With this in mind, we are ready to begin our journey through the extant literature.

The aesthetic triad

Emotion–valuation

Given the importance of facial beauty in human interactions, much research has focused on understanding its effects on human behavior. From an evolutionary perspective, physical attractiveness, including facial beauty, may signal fertility, gene quality, and health,[30–33] as reflected in the preference both sexes express for attractive people as partners.[34–37] Importantly, however, recent evidence suggests that, aside from stable developmental cues such as masculinity that drive attractiveness judgments (of men among women), short-term variable health cues such as skin color also play important roles in judgment, as do other traits, such as perceived intrasexual competitiveness.[38–40] In other words, what is deemed an attractive face appears to reflect the interplay between multiple factors, some of which are developmentally stable whereas others are plastic and likely context specific.

Researchers have also investigated the neural systems that underlie evaluations of facial beauty. An early positron emission tomography (PET) study demonstrated that rating faces on attractiveness increased regional cerebral blood flow in a network including the frontal cortex, the frontotemporal junction, the orbitofrontal cortex (OFC), the caudate nucleus, and the visual cortex.[41] The authors argued that the involvement of these regions was a specific example of their more general role in evaluative judgments involving an affective component. In other words, attractive faces were rewarding stimuli that elicited emotional responses. Several subsequent fMRI studies have confirmed this interpretation, linking attractiveness judgments to a number of structures implicated in evaluative judgment or reward processing, including the nucleus accumbens, the dorsal striatum, and the OFC.[42–44] In fact, a system involving the orbitofrontal and striatal neurons may underlie valuation of rewards irrespective of the modality giving rise to the rewarding stimuli.[13] In this sense, attractive faces could be considered just one example of rewarding stimuli that elicit activation in these regions.

A similar picture emerges when we broaden our focus beyond beautiful faces to also include other stimuli capable of producing positive-valence appraisals. For example, Brown and colleagues conducted a large quantitative meta-analysis of 93 fMRI and PET studies of positive-valence appraisal across sensory modalities, with the aim of highlighting regions reliably activated by the appraisal of the valence of perceived objects in the visual, auditory, gustatory, and olfactory domains.[45] The researchers intentionally focused on different sensory modalities because they were motivated to find core processes underlying aesthetic evaluation. In addition, within each modality they included a wide range of stimuli. For example, within vision, they selected studies that involved evaluations of pictures, artworks, images of food, erotic images, and images of loved ones (such as infants and romantic partners). Their results demonstrated that the region activated most consistently across all four modalities was the right anterior insula—a region in the brain's core affective system strongly associated with visceral perception and the experience of (negative) emotions (Fig. 1).[46,47] The authors argued that, at its core, aesthetic judgment consists of the appraisal of the valence of perceived objects. In addition, the neural system deployed for this purpose likely originally evolved for the appraisal of objects of survival advantage (e.g., food), and was later co-opted for the experience of objects that satisfy social needs, such as artworks.

Activation of the same region of the brain is necessary but not sufficient evidence to claim that a common currency underlies preference in different modalities or for different objects. Advances in imaging methods allow interrogation of patterns of activity to determine if different objects can be classified by their patterns of activation within a region. Using such analytic techniques, Pegors and colleagues examined the neural response to faces and places.[28] They found evidence for a common currency for preference in the ventromedial prefrontal cortex but selective activation for facial attractiveness in the lateral OFC, suggesting that the brain harbors neural systems for common and for domain-specific evaluations.

An interesting finding emerging from the work on faces and artworks is that the pleasure that people derive from looking at beautiful objects automatically taps into our general reward circuitry.[48] For example, attractive faces activate the fusiform face area (FFA) and parts of the ventral striatum, even when people are not thinking explicitly about the

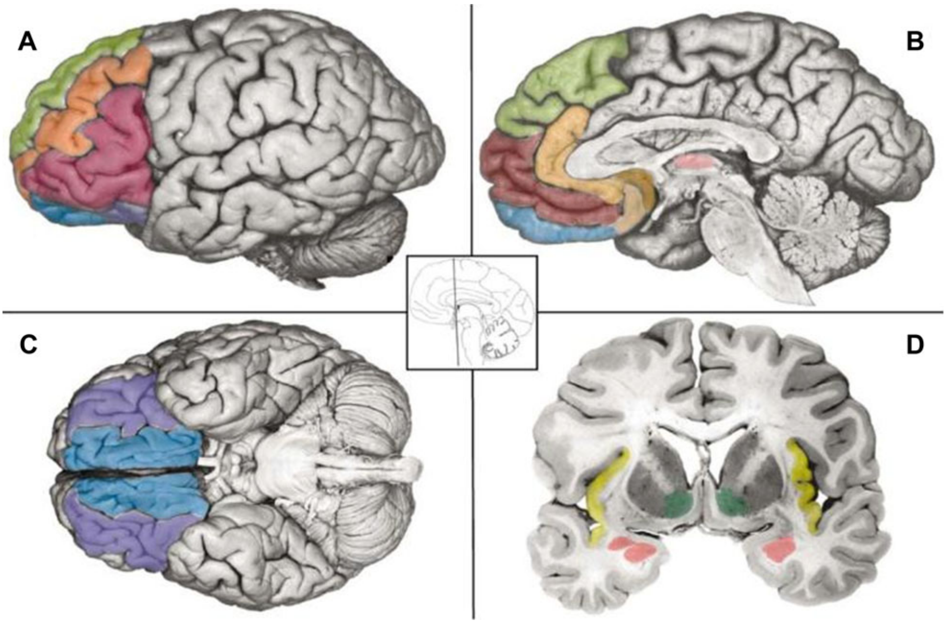

Figure 1. Key brain areas for the mental representations of emotion. The ventral system for core affect includes two closely connected circuits that are anchored in the orbitofrontal cortex (the entire ventral surface of the front part of the brain lying behind the orbital bone above the eye; (C)). The more sensory system involves the lateral sector of the orbitofrontal cortex (OFC) and includes the lateral portions of BA 11 and 13, BA 47/12 (A and C, purple). It is closely connected to the anterior insula (D, yellow) and the basolateral (BL) complex in the amygdala (D, rose in the ventral aspect). The visceromotor circuitry includes the ventral portion of the ventromedial prefrontal cortex (VMPFC), which lies in the medial sector of the OFC (A, B, and C, blue) and includes medial BA 11 and 13 ventral portions of BA 10, as well as BA 14, where the medial and lateral aspects of OFC connect; the VMPFC is closely connected to the amygdala (including the central nucleus (D, rose in the dorsal aspect)) and the subgenual parts of the anterior cingulate cortex involving the anterior aspects of BA 24, 25, and 32 on the medial wall of the brain (ACC (B, copper and tan)). The dorsal system is associated with mental state attributions, including the dorsal aspect of the VMPFC corresponding to the frontal pole in BA 10 (B, maroon), the anterior ACC (peach), and the dorsomedial prefrontal cortex (DMPFC) corresponding to the medial aspects of BA 8, 9, and 10 (A and B, green). The ventrolateral prefrontal cortex (VLPFC) is shown in red (A). Also shown for reference are the thalamus (B, light pink), the ventral striatum (D, green), and the middle frontal gyrus in the dorsolateral prefrontal cortex (A, orange). Reprinted, with permission, from Ref. 46.

attractiveness of the faces.[49,50] Along similar lines, it is important to note that structures involved in visual perception can also contribute to the computation of value and preferences. For example, not only is the parahippocampal gyrus (PPA) involved in scene perception, but its activity while viewing scenes is correlated with pleasure.[51] Specifically, Biederman and colleagues observed that cortical μ-opioid receptor density is greatest in those parts of the ventral visual pathway that process "stimuli that contain a great deal of interpretable information."[52] This suggests that 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. Importantly, the interpretation of this and similar findings must be accompanied by caution in order to avoid reverse inference, because neurotransmitter systems and brain structures typically subserve multiple mental functions. Nevertheless, the issue of how much and what kind of valuation occurs in sensory cortices is an area of active inquiry and holds great promise for advancement in the field of neuroaesthetics.

Sensory–motor

Aesthetic evaluation can engage regions of the brain that underlie sensation and perception. This inference was borne out by a recent quantitative meta-analysis based on 15 fMRI studies that involved viewing of paintings, regardless of task instructions.[53] The results demonstrated that viewing paintings activated a distributed network of structures in the brain, each likely contributing a specific component to the overall experience of viewing artworks. Perhaps not surprisingly, viewing paintings activated regions in the visual cortex, including the lingual gyrus and the middle occipital gyrus, as well as the fusiform gyrus. These activations can be attributed to the processing of various early, intermediate, and late visual features of the stimuli embedded within paintings, including orientation, shape, color, grouping, and categorization.[54–56] Although not located in the occipital lobes, the inferior temporal cortex has a well-established role in visual representation of form and color[57] and likely contributes to these processes while viewing paintings as well. Additional activation was also observed in the precuneus, likely due to the visuospatial exploration of pictorial stimuli.[58,59] The role of the visual cortex in aesthetic experience is further supported by activation in visual motion area MT+ when subjects view dynamic paintings that evoke a subjective sense of movement, such as Van Gogh's work.[60]

The meta-analysis also revealed activation in the fusiform gyrus and the PPA. The fusiform gyrus is involved in object perception and recognition, and its activation likely represents the detection of objects within paintings (e.g., faces).[61,62] In turn, the PPA is involved in the perception and recognition of places,[63] which explains its involvement while viewing paintings rich in representations of scenes (e.g., landscapes). Also activated was the anterior temporal lobe (i.e., superior temporal gyrus), a region within the temporal lobes involved not just in semantic memory—including our knowledge of objects—but also in higher-order conceptual integration of information in relation to objects (e.g., how does a knife function?).[64–66] Its activation while viewing paintings suggests that the perception of paintings might trigger higher-order semantic analysis of the represented objects beyond mere recognition.

Just as in the meta-analysis by Brown and colleagues,[45] viewing paintings also activated structures involved in emotion and/or reward processing, including the anterior insula bilaterally, as well as the putamen, a structure in the basal ganglia reliably activated by the anticipation of rewards.[67] Its involvement in viewing paintings could signal their perceived rewarding properties.

Aside from activating regions of the brain that underlie sensations and perceptions, viewing paintings that depict actions can also engage the motor system. This engagement taps into the extended mirror neuron system. First discovered in a region of the macaque monkey's premotor cortex, mirror neurons were found to respond both when the monkey performed an action and when it observed a similar action being performed by another agent.[68] A similar system that extends beyond the motor cortex has since been discovered in humans.[69] This system is engaged 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.[70,71]

A recent study by Ticini and colleagues presents some of the strongest evidence in support of the hypothesis that there is a close mirroring of motor activity between art production and art reception.[72] They asked their participants to rate pointillist-style paintings featuring discernible brushstrokes on a liking scale. Each painting was preceded by either a compatible prime consisting of a static image depicting a hand holding a paintbrush with precision, an incompatible prime depicting a hand holding a power grip, or a control prime depicting a hand resting palm down on a table. The authors hypothesized that if action simulation were causally involved in art perception, then participants would like the artwork in the compatible condition the most. This hypothesis was supported, suggesting that involuntary covert painting simulation on behalf of perceivers contributes to aesthetic appreciation.

Indeed, Freederg and Gallese have argued that our understanding of aesthetic experiences would be incomplete without seriously taking into consideration the role of the mirror neuron system in the process.[73] Empathetic responses to paintings engage our emotional circuitry, mirroring the emotions expressed in artwork.[70,73] Their view challenges some historical approaches in empirical aesthetics that give the cognitive apparatus a primary driving role in aesthetic experiences.[74] Interestingly, to the extent that artists are consciously or unconsciously aware of viewers' body-induced emotional and felt motoric responses to artworks, this knowledge can in turn be used to produce viscerally engaging art.

Meaning–knowledge

There is growing evidence that top-down processes in the form of meaning and knowledge exert strong influences on aesthetic experience. For example, original artworks are valued more than copies,[75] consistent with our intuitive dislike for forgeries. This observation suggests that our experience of art is influenced by factors beyond its perceptual qualities and involves the context within which it is processed. Along similar lines, knowing the title of an artwork facilitates greater engagement with and deepening of aesthetic experiences,[76,77] presumably by guiding how the content of the artwork is processed.

Recently, that issue was tackled directly by Gerger and Leder,[78] who presented subjects with artworks accompanied by three different title types: semantically matching, semantically nonmatching, and an "untitled" control condition. According to fluency theory,[79,80] positive aesthetic experiences are driven by processing ease. Accordingly, semantically matching titles in which the titles reference the content of the paintings in an unambiguous manner can be considered fluent because they facilitate processing, whereas the reverse would be true for semantically nonmatching titles. In addition, while subjects viewed artworks, the researchers also obtained facial electromyographic (fEMG) recordings over the *M. corrugator supercilii* and *M. zygomaticus* major muscles to measure subtle changes in emotional and cognitive processing. Liking ratings were higher in the matching and control conditions than in the nonmatching condition. However, only in the matching condition was *M. zygomaticus* more strongly activated. This finding shows that, in the matching (i.e., fluent) condition, higher aesthetic ratings are associated with positive emotions, suggesting a possible causal mechanism for how entitling affects preference.

Several investigations have examined the neural correlates of the effects of context on aesthetic experience. Kirk and colleagues presented subjects in the fMRI scanner with abstract images that were labeled as having been sourced from a prestigious Danish museum (Louisiana) or computer generated.[81] Subjects rated the images as aesthetically more pleasing if they were thought to be from the museum than if they thought they were computer generated. This preference was accompanied by greater neural activity in the medial OFC and ventromedial prefrontal cortex, regions strongly associated with the experience of reward and emotion. In addition, thinking that a painting was from a museum also produced greater activity in the temporal pole and entorhinal cortex. This suggests that contextual information can activate memories that in turn modulate levels of visual pleasure.

Another study presented subjects with paintings from the Museum of Modern Art (MoMA) that were labeled as being either from the MoMA or from an adult education center.[82] The results revealed greater neural activation in the left precuneus and superior and inferior parietal cortex for the MoMA condition compared to the control condition. When taking the aesthetic preference for a painting into account, the MoMA condition elicited higher involvement of the right precuneus, bilateral anterior cingulate cortex, and temporoparietal junction. Of particular interest is the activation observed in the precuneus, which was also involved in the study by Huang and colleagues where subjects viewed portraits that were labeled as authentic Rembrandts or fakes.[83] In that study, authentic portraits evoked greater OFC activity, whereas fakes evoked neural responses in the frontopolar cortex and the right precuneus. This suggests that the precuneus is sensitive to the way in which objects are labeled (i.e., framed). Similarly, Lacey and colleagues found that the ventral striatum, the hypothalamus, and the OFC were activated more when subjects viewed images that were easily recognizable as works of art compared to images that were matched with the art images in terms of content, suggesting that the status of an image as a work of art irrespective of its visual content can activate the reward system in the brain.[84] These studies suggest that what we attend to in the course of aesthetic interactions with artworks is strongly affected by our knowledge of compositional strategies, stylistic conventions, and practices.[85] In other words, the extent to which we are able to distill the semantic properties of artworks beyond merely their sensory qualities affects the engagement of neural systems in the service of aesthetic experiences.

Aesthetic experience as an emergent property

We have laid out a description of various types of aesthetic phenomena that can be loosely grouped under emotion–valuation, sensory–motor, and meaning–knowledge neural systems (Fig. 2). According to this model, aesthetic experiences are

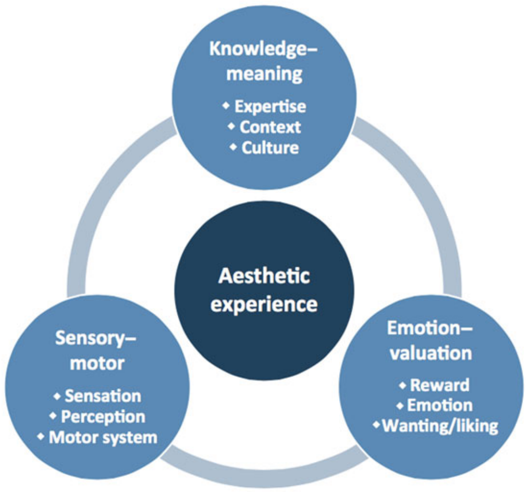

Figure 2. The aesthetic triad. According to our framework, aesthetic experiences are an emergent property of the interaction of the sensory–motor, emotion–valuation, and knowledge–meaning neural systems. Reprinted, with permission, from Ref. 8.

emergent mental states arising from the interaction of the aforementioned three neural systems. In addition, the mechanisms by which these systems influence one another in aesthetic experiences likely mimic their interactions in nonaesthetic engagements with objects.

According to our model, aesthetic experiences can encompass explicit aesthetic judgments, but are not limited to them. This is consistent with the model of aesthetic experience proposed by Leder and colleagues, which also distinguishes between aesthetic judgments and aesthetic emotions as two independent outputs of a system that underlies aesthetic experience: whereas aesthetic judgments arise from the evaluation of one's interpretation of an object (i.e., understanding), aesthetic emotions reflect the subjective ease with which an object was processed.[86] This explains why it is possible to have an aesthetic experience in the absence of explicit evaluation. Specifically, aesthetic emotions, as by-products of how we interact with objects, can lead to aesthetic experiences without the necessity of explicit judgment.

Our integrated view builds on models that frame aesthetic experiences as the products of sequential and distinct information-processing stages, each of which isolates and analyzes a specific component of a stimulus (e.g., artwork).[54,86] Historically, this sequential approach has proven useful for isolating the neural systems that underlie distinct aspects of information processing in the service of aesthetic experiences. For example, in the domain of visual art, distinct aspects of our early perceptual processing have been mapped onto specific parts of the temporal lobes, such as motion in area V5. However, recent evidence suggests that these three systems can interact early in the service of forming an aesthetic judgment, rather than exerting their effects sequentially. For example, electroencephalographic (EEG) evidence suggests that sensory (bottom-up) and contextual (top-down) integration occurs within 200–300 ms of seeing an artwork.[87]

Importantly, the three systems need not necessarily contribute to aesthetic experiences in equal measure. Some aesthetic phenomena can be explained without any reference to emotion,[74] and aesthetic responses to mathematics would appear to be devoid of sensations.[88] Nevertheless, it appears that under certain conditions even seemingly highly intellectual and abstract stimuli can engage the brain's reward system. For example, Zeki and colleagues have recently shown that, among mathematicians, the experience of mathematical beauty correlates parametrically with activity in the medial OFC, a region activated by other sources of beauty.[89] These findings suggest that we have much to learn about the contribution of the meaning–knowledge system to aesthetic experiences. In part, this might be because the meaning–knowledge system has a relatively more distributed representation throughout the brain than do the emotion–valuation and sensory–motor systems. In addition, the representations of meaning and knowledge likely vary greatly across individuals, cultures, and historic epochs,[22] which in turn would introduce more variability in the neural representation of those factors.

In addition, our current understanding of the neural systems that underlie aesthetic emotions is limited by the study of generally mild and pleasant aesthetic encounters, despite the fact that people are known to experience aesthetic emotions that can vary greatly in valence and/or intensity (e.g., horror, disgust). Perhaps equally importantly, we know very little about the aftereffects of aesthetic encounters. This is somewhat puzzling because our own experiences suggest that our encounters with artworks in museums and art galleries can have strong and lasting effects, long after the interactive episodes have elapsed. However, inroads into the

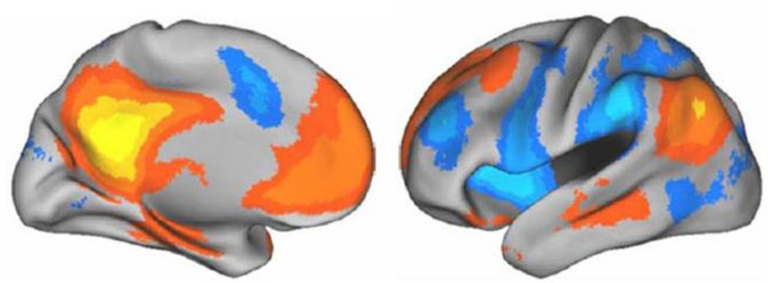

Figure 3. The default mode network (DMN) and the external attention network in the brain. The DMN is represented in orange, whereas the external attention network is represented in blue. These two networks are anticorrelated: as activity within the DMN increases, activity in the external attention network decreases. Reproduced under the terms of the Creative Commons Attribution License from Ref. 188.

neural bases of these types of problems are being made.[90]

Aesthetic experience: uniformity versus variety

Depth of processing

Not all aesthetic experiences feel alike: whereas some are subtle and fleeting, others can have profound and gripping effects on the person.[91,92] Why is that? Consideration of this issue has become increasingly important as empirical aesthetics extends beyond a focus on transient emotions to intense aesthetic experiences that many perceivers actively seek. Leder and colleagues proposed an influential information-processing model of aesthetic experience, which is postulated to emerge as a function of information processing along five stages: perception, implicit classification, explicit classification, cognitive mastering, and evaluation—ultimately producing aesthetic judgments and aesthetic emotions as its output.[86] According to this model, depth of processing is likely a function of the extent to which information is processed in later stages of the information-processing sequence. This view shares similarities with Graf and Landwehr's recently proposed dual-process perspective on fluency-based aesthetics.[93] As its dual-process terminology implies, stimuli can be processed aesthetically using automatic or controlled processes, with the relative contribution of the two systems determining the depth of aesthetic experience. Specifically, their model suggests that processing performed immediately upon encountering an aesthetic object (i.e., the perception and implicit classification stages of Leder and colleagues) is bottom-up and stimulus-driven, giving rise to aesthetic evaluations of pleasure or displeasure. In turn, assuming that the stimulus affords it and there is sufficient processing motivation on the part of the perceiver, more elaborate top-down processing can emerge, giving rise to fluency-based aesthetic evaluations (e.g., interest, boredom, confusion).

The idea that deep aesthetic moments can arise while viewing artworks is supported by the observation of the involvement of the default mode network (DMN) in aesthetic states. Activity in the DMN is observed when individuals are not engaged in goal-directed behavior.[94] Indeed, brain activity in the DMN is anticorrelated with brain activity observed in the external attention network, which comes online when people are engaged in goal-directed behavior involving external stimuli (Fig. 3). In this sense, the DMN is active when we engage in internally generated rather than externally driven thought.[95,96]

It has recently been shown that the DMN is engaged when people view paintings that they regard as particularly moving. Specifically, Vessel and colleagues presented their subjects with a variety of paintings and asked them to rate each using a 1–4 scale that asked, "How strongly does this painting move you?" The wording of the question was purposeful, meant to tap into deeper, internally oriented aesthetic experiences. Their analyses revealed suppressed deactivation of regions that constitute the DMN when subjects viewed paintings that they rated as most moving (i.e., level 4)—including the medial prefrontal cortex and the posterior cingulate cortex.[97,98] These results suggest that deeper aesthetic moments are associated with an internal orientation.

Consistent with the notion that aesthetic experiences include an internally oriented component, subjects focusing on the feelings that artworks evoke exhibit activation of the insulae,[58] regions strongly implicated in regulating our autonomic nervous system and the visceral experience of emotions (Fig. 1). The results from these studies suggest that, within the context of viewing art, an internal focus has two distinct connotations—one that includes self-referential processing of autobiographical and narrative information and another that represents more visceral feeling states (i.e., interoception).[99] In turn, these two connotations have dissociable neural representations in the DMN and the insulae, respectively. The involvement of the DMN while viewing paintings was borne out further by the results of a meta-analysis of viewing paintings, which revealed activation in the posterior cingulate cortex bilaterally.[53] This region has emerged as a key component of the DMN.[96,100] The emergence of this area across studies suggests a novel angle in the study of paintings by highlighting a process that many consider essential to deep appreciation of artworks, namely a focus on inner emotions and thoughts.

Data consistent with the notion that aesthetic stimuli might be processed at deeper versus shallower levels have emerged from neuroimaging methods that allow examination of the temporal aspects of aesthetic evaluation, such as magnetoencephalography (MEG). MEG enables the assessment of neural responses with a temporal fidelity not possible with fMRI. Cela-Conde and colleagues used MEG to study the functional connectivity dynamics underlying aesthetic appreciation. Specifically, they focused on early and delayed temporal epochs following the presentation of stimuli—one within 250 ms and one between 1000 and 1500 ms, respectively.[101] The authors found dissociable patterns of neural activity and connectivity in relation to early and delayed phases. Importantly, activity in the DMN corresponded mainly to the delayed phase. The authors argued that, whereas the early phase of aesthetic evaluation involves rapid judgment of a stimulus as "beautiful" or "not beautiful," it is the delayed phase that engages a deeper level of processing in terms of why we find a stimulus beautiful. In this sense, the delayed MEG response may reflect the effects of cognitive appraisals on emotional experiences with artworks (i.e., controlled top-down processes). This interpretation is consistent with the appraisal theory of emotions, according to which subjective goals and desires influence emotional reactions to objects and events in the world.[102] This can also help explain why the same works of art can evoke radically different responses in viewers in terms of the top-down appraisals that are applied to initial judgments.[103]

An interesting recent study suggests that even elementary perceptual features trigger aesthetic experience along neural paths that vary in automaticity. Ikeda and colleagues presented subjects in the fMRI scanner with color pairs that were harmonious or disharmonious.[104] Harmonious pairs are typically perceived to be pleasant, whereas disharmonious pairs are perceived to be unpleasant. They found that, whereas harmonious color pairs activated the medial OFC, disharmonious color pairs activated the amygdala. In conjunction with detailed psychophysical analyses, the authors suggested that color disharmony is driven by bottom-up stimulus properties that automatically trigger activation in the amygdala, whereas processing color harmony may depend more on evaluative processes represented by activation in the medial OFC. Although further work is clearly necessary to determine whether the neural basis of aesthetic experience can diverge at such an early stage, Ikeda *et al.*'s results suggest that possibility.

Recent neuroimaging work on special aesthetic states has also involved studying brain activation in relation to the experience of the sublime—a construct of great importance in philosophical treatments of aesthetics. Although our understanding of the sublime has changed over the last centuries, it is generally believed to be experienced while in the presence of natural scenes of grandeur, involving anxiety mixed with a sense of beauty. As such, sublime experiences tend to evoke awe and engage the imagination. Ishizu and Zeki previously conducted an fMRI study to show that a region in the medial OFC is sensitive to variations in judged beauty across modalities (i.e., paintings and music).[105] Indeed, a cluster consisting of the orbito- and medial-frontal cortex, ventral striatum, anterior cingulate, and insula has been shown to respond to beautiful visual images,[106–108] as well as sources of pleasure, including architectural spaces.[109] Switching to the sublime, Ishizu and Zeki examined whether it would activate the same brain region as the one most consistently activated in their studies of beauty, namely the medial OFC.[110]

Before the scans, subjects rated photographs of natural scenes on sublimity, including pictures of mountains, falls, forests, volcanoes, tornadoes, ocean waves, glaciers, clouds, and deserts. This enabled the researchers to select, for each subject, stimuli that they had themselves rated as very sublime and not at all sublime. The fMRI results revealed a distinctly different pattern of brain activity from that obtained for the experience of beauty. Specifically, viewing sublime images activated the inferior temporal cortex, the posterior hippocampus, and the inferior/middle frontal gyri, in addition to subcortical areas including the basal ganglia (caudate and putamen) and the cerebellum; deactivations were observed in the cingulate cortex/medial prefrontal cortex, the anterior superior temporal sulcus, the cerebellum, and the caudate. Critically, none of the activated regions overlapped with the mOFC, where activity correlates parametrically with the experience of beauty. Moreover, the distributed pattern of activation corresponded with the authors' conception of the sublime as a "distinct cognitive–emotional complex, which involves many components but is distinct from each individually."

Individual differences in taste

Although some neuroimaging studies of aesthetic experience have explored group differences in brain activation as a function of sex[111–113] or levels of expertise (see below), we know little about the neural correlates of individual differences in aesthetic processing. This is a curious state of affairs given our intuition that people differ in their aesthetic preferences. Take facial attractiveness, for example: judgments between two raters correlate in the range 0.3–0.5.[114] This accounts for only 9–25% of the variance observed in attractiveness ratings. Hönekopp has shown that, when assessing facial attractiveness, our taste is determined in approximately equal measure (≈50%) by what we find uniquely beautiful (private taste) as by what we find commonly beautiful (shared taste).[115] Extending this logic, more research needs to be conducted that focuses on the neural basis of individual differences in aesthetic experience.

Recently, some inroads have been made in exploring the neural basis of individual differences in perceived facial attractiveness. Specifically, researchers used fMRI to compare participants who on average gave higher versus lower attractiveness ratings to faces.[116] This comparison reflects fine-tuning or parameter setting relative to a group of stimuli and represents individual differences in the metric used to assess facial beauty. The comparison activated the right middle temporal gyrus (MTG). Interestingly, unlike the FFA, the superior temporal sulcus, and the occipital face area, the MTG is not one of the three main cortical regions involved in face perception in humans.[62] Rather, it appears to play an important role in integrating information across modalities.[117] Its activation in relation to individual differences suggests that judgment of facial attractiveness might rely on integration of information from a variety of sources extending beyond the domain of faces exclusively, including relevant semantic, emotional, social, and cultural factors.

People exhibit greater individual differences in their preferences for art compared to preferences for real-world images, for which there is more uniformity of judgment.[118] Indeed, one method for allowing individual differences to emerge is to present subjects with paintings that depict a very wide variety of styles and periods, and then use subjective ratings to create individual response profiles. Using such an approach, Vessel and colleagues used fMRI to demonstrate that 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.[97,98] Interestingly, as was shown to be the case with facial attractiveness, here there also appeared to be a neural dissociation between regions of the brain that respond to individual differences in awe and pleasure versus those that are activated by aesthetic judgment across individuals. This suggests that shared and private components of aesthetic experience can be parsed at a neural level, although the functional significance of these different neural structures remains to be worked out.

Expertise and formal training

One of the most reliable findings to emerge from empirical aesthetics is that expertise and formal training in the arts influence aesthetic experience, quantifiable both in terms of subjective ratings and viewing patterns measured by eye tracking.[119,120]

For example, much evidence suggests that, whereas naive subjects prefer representational over abstract paintings, this effect is attenuated or absent among subjects with formal training in the arts.[121] This effect has been interpreted to mean that people with formal training have acquired the skills to interpret and distill meaning in abstract art, which in turn can lead to aesthetic pleasure. However, it is important to note that, while expertise can lead to greater levels of understanding and interest, it does not necessarily affect emotional appraisals of art.[122] In this sense, expertise might exert dissociable effects on cognitive versus emotional aspects of aesthetic processing. In addition, data have shown that, whereas the preference level of naive subjects is strongly influenced by the level of abstraction and surface features of paintings (e.g., color palette), experts are more sensitive to the underlying structural features of artworks (e.g., compositional balance). Taken together, the behavioral and eye-gaze data have demonstrated that experts and laypersons pay attention to different aspects of paintings.[123]

Recent studies have begun to investigate the neural correlates of expertise in aesthetic experience. Else and colleagues measured event-related potentials (ERPs) while artists and non-artists viewed and rated representational, abstract, and indeterminate 20th-century art on how much it affected them.[124] Their results revealed that N1 and P2 waveforms were enhanced among artists compared to nonartists, especially in relation to abstract art. This suggests greater levels of attention/effort and higher-order visual processing among experts in the course of aesthetic judgment. However, it is important to highlight that expertise-related effects on brain activity can vary as a function of the task. For example, Pang and colleagues presented paintings to subjects who varied in their expertise.[125] Critically, they instructed their subjects to engage in free viewing of the artworks without the need to make any assessment. They found that art expertise correlated negatively with the amplitude of the ERP responses to paintings in posterior brain regions, leading the authors to conclude that extensive practice in the contemplation of visual art among artists leads to greater neural efficiency. Additional research with fMRI in the domain of architecture has shown that, compared to non-architecture students, architecture students recruit fewer brain structures for encoding and detecting building stimuli.[126] This finding also suggests that expertise might confer an advantage in terms of neural efficiency in visual processing.

However, expertise appears to exert domain-specific effects on brain activation. For example, Kirk and colleagues measured brain activation while architects and non-architects viewed and rated pictures of buildings and faces on aesthetic preference.[127] The results demonstrated greater activation among experts in the subcallosal cingulate gyrus and medial OFC when making aesthetic judgments of buildings, but no difference was detected while making similar judgments of faces. This suggests that expertise in architecture modulates the neural representation of value in the reward network only for domain-relevant stimuli (i.e., buildings).

Beyond random polygons

Having reviewed earlier work in empirical aesthetics, Silvia asked, "Why would someone think that studying how undergrads rate random polygons tells us anything about the human experience of the arts?"[103] This is a legitimate question, because it is difficult to reconcile the feeling of awe one has when experiencing works of great aesthetic significance with the feelings evoked when viewing and rating simplified stimuli under laboratory settings. This is not to say that principles derived from the study of nonart stimuli cannot contribute to our understanding of our interactions with artworks. In fact, much of the structural skeleton of contemporary models of aesthetic experience is built on data gathered from simplified stimuli. Rather, there is a strong sense that the field needs to move beyond beauty and simple preference to gain traction on more fully realized aesthetic experiences that grip art audiences, including those mediated by sadness, fear, interest, and surprise.

Expressionist theories of art emphasize the ability of art to communicate subtle emotions that are difficult to convey with words.[128,129] Recently, neuroaesthetic studies of nuanced emotions beyond simple preference have begun to surface.[108] These studies could prove especially fruitful for understanding aesthetic experiences involving emotions that vary in valence as well as intensity. For example, the "delicate sadness" evoked by Noh masks used in traditional Japanese theater has been shown to engage the right amygdala.[130] We are also beginning to learn more about the neural bases of negative aesthetic impressions. For example, Munar and colleagues used MEG to study brain activity when subjects viewed and rated a diverse array of visual images as beautiful or not beautiful.[131] The authors observed that activity in the right lateral OFC within 300–400 ms following the presentation of the stimulus was greater for images rated as not beautiful than as beautiful. Consistent with findings from a MEG study performed by Cela-Conde and colleagues, where an initial burst of activity was associated with early aesthetic impression formation,[101] the authors argued that the early activity observed in the lateral OFC represents a rapid judgment of visual stimuli as aesthetically not pleasing.

Recently, Era and colleagues measured the effects of subliminally presented positive, negative, and neutral primes on beauty and emotion judgments involving abstract and body images.[132] Interestingly, they found that, in comparison with positive primes, negative primes increased subjective aesthetic evaluations of both types of target images. Importantly, primes had no effect on emotion judgments, which ruled out any nonspecific arousal effect on judgments. By demonstrating that negative emotions can enhance positive aesthetic evaluations, their results reinforce the notion that aesthetic experiences are facilitated in nuanced ways by not only positive but also negative emotions.

Focusing on music, Sachs and colleagues drew on a large corpus of neuroimaging and patient data to propose a homeostatic model for explaining how sadness can lead to the experience of pleasure.[133] Homeostasis refers to the process of maintaining internal conditions within a range that promotes optimal functioning, well-being, and survival. Within this view, emotions are considered mechanisms evolved to reestablish homeostatic equilibrium, and feelings of pleasure constitute the psychological reward for having achieved homeostasis. According to this framework, music-evoked sadness can lead to pleasure if three conditions are met. First, the sadness evoked by music must be perceived as non-threatening. In this sense, the context within which the sadness is experienced is key. Second, it must be perceived as aesthetically pleasing. Finally, it must lead to psychological benefits, including evocation of memories, empathy, and mood regulation. In turn, the realization and interplay of these conditions can be influenced by other background factors (e.g., personality).

Although this model was proposed in relation to sadness in music, it could be used to explain similar aesthetic phenomena in other domains. For example, why do people experience pleasure when viewing horror movies in cinemas, whereas the experience of fear is typically not pleasurable? It would appear that this setting could meet all three conditions outlined in the model proposed by Sachs and colleagues. First, context is critical, such that within the confines of movie theatres fear is perceived as nonthreatening. Second, within that context fear can be perceived as aesthetically pleasing. Finally, there is reason to believe that in some people these experiences are accompanied by psychological benefits, such as mood regulation. Importantly, the satisfaction of these conditions is not a guarantee that everyone will accrue similar benefits from the experience. As with music, no pleasure might be experienced if either no homeostatic imbalance was present to begin with or the stimuli failed to correct the imbalance (e.g., no memories were evoked).

Another interesting model that has been proposed to explain our ability to derive pleasure from exposure to film and literature involves Gallese and colleagues' notion of *liberated embodied simulation.*[134,135] Embodied simulation is defined as a property of the human brain whereby the actions, emotions, and sensations of others are mapped onto one's own sensory–motor and visceromotor neural representations. As a result, the observation of an action/emotion/sensation can trigger the activation of the same neural mechanisms involved in their execution in the observer. In the context of aesthetic experiences, these embodied simulations can become liberated. Specifically, because the aesthetic context places the external world at the periphery of attention, one's simulative resources are freed to engage more strongly with the stimulus, be it film or literature. As such, rather than serving to suspend belief, aesthetic context can serve to augment the strength of one's interactions with artworks.

Finally, context effects along the lines described above are also informative in helping to explain why not all appraisals of valence are necessarily aesthetic in nature. Specifically, the context within which an object is encountered can influence whether one is motivated to appraise its valence aesthetically or not. Indeed, we believe that examining the effects that contexts and motivations exert on the appraisal of objects varying in valence and intensity represents an important area of inquiry within neuroaesthetics.

Disinterested interest: liking without wanting?

Why do we desire rewards? For most people, rewards are desirable because obtaining them leads to a conscious experience of pleasure. In this sense, rewards are perceived to have *incentive salience*, meaning that they are accompanied by a motivation to approach and consume the rewards.[136] In fact, for this very reason, rewards are defined by their ability to alter behavior. However, it has been hypothesized that deep aesthetic encounters with artworks are distinguished from interactions with other types of rewarding stimuli precisely because they do not mobilize a similar motivational stance. For example, 18th-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 an accompanying desire to acquire, control, or manipulate it. If true, what might the neural correlates of disinterested interest be?

Interestingly, human neuroimaging studies have shown that, whereas the experience of "wanting" in the pursuit of a reward activates a large and distributed system in the brain, "liking" or pleasure itself is underpinned by a rather small set of hedonic hot spots within the limbic system.[137] It is perhaps even more surprising that a diverse set of pleasures—including those derived from food, drink, sex, addictive drugs, friends, loved ones, music, and art—activate the same limbic hot spots in the brain. Typically, pleasure and reward work in concert and have overlapping neural circuitry, especially within the ventral striatum. This explains why we tend to want what we like. However, as research by Berridge and colleagues has shown,[138] this need not necessarily be the case. This dissociation can be highlighted in addictions, where there can be wanting (i.e., craving) without necessarily liking (i.e., pleasure in consumption). The Berridge distinction resembles that of Ortony and colleagues between object-related and outcome-related emotions.[139] In this sense, aesthetic emotions (e.g., pleasure, repulsion) are triggered by objects, in contrast to emotions triggered by outcomes (e.g., happiness, disappointment).[45] The mental state of disinterested interest may reflect activity in the liking system without activity in the wanting system.[88]

Although the aforementioned hypothesis remains to be tested in humans engaged in aesthetic encounters, some recent behavioral evidence suggests that experts may be more capable of adopting a stance reflective of disinterested interest than novices. Specifically, Leder and colleagues investigated how positively and negatively valenced artworks affect aesthetic and emotional responses in viewers, measured using self-reports and fEMG, respectively.[140] The results demonstrated that expertise moderated the effects of emotional valence on ratings and fEMG. Specifically, compared to laypeople, experts showed less corrugator activation in response to negative stimuli as well as less relaxation in response to positive stimuli. Switching to valence ratings, there was a trend for experts toward providing less extreme valence ratings of negative and positive works of art. The same patterns were observed in relation to pictures from the International Affective Picture System (IAPS). These findings are consistent with the Kantian notion that adopting an aesthetic stance is emotionally distanced, at least among people knowledgeable about the visual arts. We believe that continued work on this issue will likely prove useful in explaining how pleasurable aesthetic responses are a particular subset of rewarding experiences distinct from desires for objects that drive consumer behavior.

Art production

Descriptive neuroaesthetics

Descriptive neuroaesthetics refers to scholarship that applies principles of psychology and neuroscience to aesthetic concerns. This approach contrasts with experimental aesthetics, which tests hypotheses using experimental methods. Classic examples of descriptive aesthetics come from early neuroaesthetic writings that identify parallels between the approach of artists to their visual world and brain processing of visual information. For example, Zeki grounded visual aesthetic appreciation strongly within visual perception, describing how the neuroanatomical specialization of the visual cortex, in terms of processing specific features of percepts (e.g., form, color, motion), contributes to our processing of content in artworks.[23] Following the same logic, he argued that artists have historically acted as naive neuroscientists, manipulating features of their artworks to induce desired responses in the nervous systems of perceivers.

A similar argument was made by Cavanagh,[141] who observed that, rather than depicting the veridical physical properties of the world, paintings reflect perceptual shortcuts used by the brain. Specifically, artists intentionally incorporate features that activate these shortcuts to facilitate desired perceptual and emotional effects in viewers. In doing so, they intentionally violate the physical laws that characterize shadows, reflections, colors, and contours. In this sense artists, in experimenting with various forms of depiction, discovered what psychologists and neuroscientists are now identifying as principles of perception. For example, paintings 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. Because people are insensitive to the contour but not the luminance of the shadows, the 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.

Indeed, artists at the turn of the 20th century homed in on different attributes of our visual brain.[24] 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.[142] 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.[143] The chicks peck more vigorously at 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.[144]

Artists also exploit the way our visual system processes information in two interacting streams.[145,146] 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 of the "where" stream's reduced sensitivity to boundaries, the objects appear to shimmer.[147]

Art production following brain damage

Neuropsychological data collected from patients have proven very useful in studying the neurological bases of art production because they enable one to test causal hypotheses that are not amenable to testing using correlational data from neuroimaging studies.[148–151] As such, patient data can be a powerful tool for rejecting hypotheses. For example, a popular notion in psychology and neurology has involved associating the right hemisphere with artistic production. This hypothesis can be tested by examining the effects of unilateral damage to the right and left hemispheres on artistic production. If this view is correct, then damage to the right hemisphere should profoundly impair artistic production, whereas damage to the left hemisphere should largely spare such abilities. To test this hypothesis, the Assessment of Art Attributes (AAA)[152] was used to assess changes in the artwork of three patients with lateralized brain damage: the Californian artist Katherine Sherwood and the Bulgarian painter Zlatio Boiyadjiev, both of whom had left brain damage, and Lovis Corinth, an important German artist who had right brain damage.[153] The AAA is an instrument designed to assess works of art along six formal–perceptual and six conceptual–representational attributes. Participants in the study rated works by the aforementioned three artists produced before and subsequent to neurological injury in random order. The results demonstrated that following injury the art of all three artists became more abstract and distorted and less realistic. In addition, all three artists painted with looser strokes, less depth, and more vibrant colors. Contrary to the notion that the right hemisphere is the dominant artistic hemisphere, no unique pattern was observed in the work of Corinth. The results demonstrated that both hemispheres participate in artistic production. This is because, by and large, the artworks of all three artists changed in similar ways regardless of which hemisphere was damaged.

Paradoxically, damage to either the left or right hemisphere can sometimes result in facilitations of artistic production and expression. For example, Corinth's large right-hemisphere stroke led to left spatial neglect, observable by his omissions of details and textures on the left of his portraits. However, these works were regarded highly by critics.[154] His premorbid images were "highly cerebral," and incorporated esoteric images of cross-dressers, medieval seals, and spy photos. In contrast, following his stroke he described his style as "raw" and "intuitive" and his left hand as "unburdened," enjoying an ease and grace with the brush that his right hand never had.[155] The right-hemisphere stroke experienced by artist Loring Hughes led to difficulty in coordinating the spatial relationship between lines, forcing her to abandon her premorbid style of realistic depictions. Instead, she relied on her own imagination and emotions for inspiration.[156] These cases demonstrate that brain damage can lead to greater imaginative and emotive expression.

Importantly, these observations are not limited to cases involving damage to the right hemisphere. For example, the premorbid artistic style of Boiadjiev was natural and pictorial, and he used earth tones. Following his stroke, his paintings were richer and more colorful, fluid, energetic, and even fantastical.[157,158]

Similar facilitations of artistic production and expression are sometimes observed in patients with frontotemporal dementia (FTD) and Alzheimer's disease (AD). Patients with FTD exhibit a wide range of deficits in memory, attention, and executive function. Importantly, these cognitive changes are typically accompanied by personality changes, such as impulsivity and obsessive–compulsive behavior. Some patients with FTD also develop a propensity to produce art. Their art is typically realistic, obsessive, and detailed.[159] This artistic output is a consequence of acquired obsessive–compulsive traits that are expressed graphically. There are other clinical examples involving artistic savants with autism that confirm the association between obsessive–compulsive traits and the propensity to produce art.[160–163] Obsessive–compulsive traits imply dysfunction of the OFC and MTL and frontostriatal circuits.[164] Notably, the posterior occipitotemporal 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.

Some artists with AD continue to paint after the onset of their illness.[165–168] 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.[169]

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 it 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.

Recently, noninvasive brain stimulation methods that use magnetic pulses or direct electrical currents to produce virtual lesions or enhancements to specific parts of the brain can also test the causal hypothesis that flexible neural ensembles underpin aesthetic experiences. This can be done by examining how changes in neural activity in local areas modulate aesthetic experiences. For example, applying anodal (excitatory) transcranial direct current stimulation to the left dorsolateral prefrontal cortex made individuals like representational paintings and photographs more than they did under sham stimulation conditions.[170] Extending earlier MEG findings,[171] these new results show that activating a region correlated with aesthetic judgments (i.e., the left dorsolateral prefrontal cortex) can influence aesthetic experience.

Aesthetics and artistic creativity: mirror images

In his recent mirror model of art, Tinio proposed a comprehensive and testable framework linking the creation and perception of art.[172] The basic premise of the model is that the temporal sequence of art perception mirrors the temporal sequence of art creation. As such, the psychological processes that the perceiver engages in during the early stages of art perception mimic the psychological processes the creator engaged in during the late stages of art creation, and vice versa. This elegant model thereby allows one to test specific hypotheses about the reverse correspondence of processes linking creation to perception.

Tinio's model is supported by extensive empirical research. Specifically, there are generally two methods for studying the stages of artistic creativity.[173] The first method involves directly observing artists at work, whereas the second method involves the retrospective study of archival material from artists. Both of these approaches converge to show that the creative process in the arts occurs along three stages. In the first stage (initialization), the artist explores the viability of various ideas. At this stage, sketching can play a key role, as it enables the artist to develop emerging ideas, leading to basic structural configuration of the painting. This basic structure is reflected in the underdrawing of the painting. In the second stage (expansion and adaptation), the artist fine-tunes and reworks the underdrawing. At this stage, the characteristics of the objects and the subjects in the painting undergo numerous changes, reflected in modifications made to specific elements of the work. In the last stage (finalizing), work on major structural elements of the artwork ceases, and time is devoted to enhancing the surface layer of the work in preparation for viewing. Here, focus is shifted to color and texture.

This model relies on the concept of layering. Specifically, the artist communicates ideas to the perceiver through various layers of materials that will be encountered in reverse order by the perceiver. Critically, the concept (i.e., initial idea) that triggered the piece is encapsulated in the work conducted during initialization and represents the final destination in the viewer's journey toward discovering the essential meaning of the artwork. This is because, when a perceiver first encounters an artwork, he/she is likely to engage in early automatic processing of low-level features such as color and contrast that are driven by the surface characteristics of the artwork—added during the finalizing stage of creation. The next stage of perception involves intermediate memory-based processing of content and style, driven by elements such as objects modified during the expansion-and-adaptation stage of creation. Finally, during the last stage that corresponds to meaning making and the generation of aesthetic judgments and emotions, the focus is on deciphering the intentions of the artist for creating the artwork, a higher-order cognitive state that draws from the structural organization (i.e., underdrawing) of the painting.

The mirror model of art represents an important organizational framework that researchers can use to explain various findings about the psychological and neurobiological bases of aesthetic experience. For example, we know that people with formal training in the visual arts report greater appreciation of abstract art than naive subjects.[121] One possibility is that naive subjects have difficulty venturing beyond the surface characteristics of abstract artworks, whereas people with formal training in the visual arts excel at accessing the underdrawing of abstract paintings, thereby discovering the essential meaning of the artwork. This hypothesis is testable at the neural level by comparing the relative engagement of sensory–motor versus meaning–knowledge structures between experts and novices. Such neurological comparisons can be augmented by chronometric data, leading to more accurate process models of aesthetic experience.

This model can also be valuable for improving our understanding of the neural bases of the various stages of artistic creativity.[174] Specifically, recent methodological advances have made it possible to study artistic creativity in action, as subjects engage in jazz improvisation,[175] creative writing,[176] and drawing[177] in the fMRI scanner. Mirroring findings from psychological studies of creativity, these data have shown that the neural bases of artistic creativity are to an extent domain specific. For example, and not surprisingly, it has been shown that creative writing engages the left-lateralized linguistic centers of the brain in the temporal and frontal lobes. However, and of particular interest for the present purposes, some researchers have studied artistic creativity in stages. For example, Shah and colleagues used fMRI data to test the hypothesis that creative writing unfolds in three stages (planning, translating, and reviewing).[176] These stages clearly correspond to the three stages of the mirror model of art, despite the fact that they are formulated in relation to a different domain. Our understanding of artistic creativity would benefit by examining the extent to which the neural bases of earlier versus later stages of artistic creativity are affected by domains. Presumably, domain-related differences should be amplified in later stages as artists execute their core ideas, but this hypothesis remains to be tested.

The evolutionary origins of art

It is perhaps only appropriate that we end at the beginning, asking what might be the evolutionary origins of art.[178,179] Most scholars of evolutionary aesthetics fall in one of two camps. Some think that art represents a universal impulse and is best regarded as an adaptation, or an instinct, embedded deep within us. Others argue that art represents an epiphenomenon of other adaptations. This view of art as exaptation emphasizes the variability and cultural contingency of artworks that do not seem to serve a purpose or a coherent final cause. How can we make headway toward solving this mystery? The example typically evoked to address this issue is the peacock's tail—evolutionary psychologists' favorite example of a costly display that advertises the bird's fitness. The tail is elaborate and beautiful, but it also makes it harder for the peacock to move quickly, leaving it vulnerable to predators. Sexual selection, rather than natural selection, drives the development of these colorful tails. Many cultural artifacts are thought to be like the peacock's tail. For some scholars, art is a prime example of a costly display, displayed as a sign of the bird's fitness.

However, an alternative analogy, also based on a consideration of bird behavior, also exists. The feral white rumped munia lives in the wild throughout much of Asia. Like many birds, its male counterpart sings stereotypic songs to attract mates. Over 250 years ago, Japanese bird breeders became interested in mating the munia for its plumage to produce birds with especially colorful feathers. In this artificial niche that emphasizes color, and over 500 generations later, the wild munia evolved into the domestic Bengalese finch. The Bengalese finch's song is now irrelevant to its reproductive success. Nevertheless, and remarkably, although it was being selected for color, its song became more complex and variable, and the sequence of notes became more unpredictable.[180] The Bengalese finches also became more responsive to their social environment. They can learn new songs more easily than their munia ancestors, and even learn abstract patterns embedded in songs.[181] As the usual selective pressures were reduced, the natural drift and degradation of genes that program the stereotypic song could occur. The contaminated genes allow for neural configurations that produce songs that are less constrained and easily perturbed. What the Bengalese finch hears in its environment increasingly influences the content of its song.

The changes in the finch's song are accompanied by changes in its brain. Whereas in the munia the neural pathways for innate songs are relatively simple and mostly controlled by one subcortical structure called the nucleus RA,[182] in the case of the Bengalese finch there exists a widely distributed neural system that is engaged more flexibly. In some ways, the difference between the munia and the Bengalese finch is analogous to the difference between playing in a prescribed manner versus improvising. As genetic control over brain function relaxed, instinctual constraints on the bird's song became less specific. The finch's brain became more flexible and its behavior more improvisational and responsive to local environmental conditions.

Thus, opposite evolutionary forces drove the emergence of the peacock's tail and the Bengalese finch's song. Ramping up selective pressures produced the tail, while relaxing these same pressures produced the song. The song started as an adaptation but evolved into its current form in a relatively short time, precisely because it no longer served an adaptive function. The art we encounter today is more like the Bengalese finch's song than the peacock's tail. Importantly, the point is not that the finch's song is art and the munia's song is not art. Rather, both songs serve as examples of the qualities of art that emerge in a given environmental niche. The relaxation of selection pressures on bird songs and art increases the variety of options available to the community. By thinking of art as the product of the alternating dynamics of selection and relaxation, we can move beyond traditional ways of thinking of art as either an instinct or an evolutionary by-product, but rather as an emergent property arising in a dynamic environmental niche.[88]

Table 1. 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 experience?
- How are different aesthetic emotions—including negative ones such as horror and disgust—implemented in the brain, and how do they 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 sex differences in aesthetic experiences?
- How does expertise in the visual arts alter the 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?
- How is taste instantiated in the brain?
- Do art perception and production serve homeostatic needs?

NOTE: Adapted from Ref. 8.

Coda

Neuroaesthetics is at a historical inflection point, ready to enter the mainstream of cognitive neuroscience. Its concerns cut orthogonally across more traditional domains, such as perception, emotion, attention, memory, and decision making. As would be expected of any emerging field, its contours are undergoing refinement.[183] Humanist scholars have questioned the ability of neuroaesthetics to shed light on our artistic experiences,[184,185] whereas others have criticized the field's narrow focus on aesthetic phenomena.[186] Importantly, as explained at the outset, the explanations provided by a neurological approach to aesthetics constitute an important component for understanding the causal structure of aesthetic experiences. In isolation, the approach has its limitations. For example, neuroscientific approaches are not ideally suited for extracting the historical, social, and cultural context within which works are produced and appreciated. As such, multimodal and interdisciplinary approaches that incorporate neuroscientific approaches would appear to be particularly fruitful for advancing our understanding of aesthetic phenomena.[187] Despite these challenges, the relevant questions are coming into focus even as the answers to many of the basic questions remain to be worked out (Table 1). Importantly, findings emerging from this field can pay dividends not only by increasing our understanding of the biology of evaluative appraisals, but also by elucidating deeper aspects of the human condition, including our likes, desires, and motivations.

Conflicts of interest

The authors declare no conflicts of interest.

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