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Review

Shaping and reshaping the aesthetic brain: Emerging perspectives on the neurobiology of embodied aesthetics

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ABSTRACT

Less than two decades after its inception, the burgeoning field of neuroaesthetics continues to grow in interest and momentum. Despite the biological and social importance of the human body and the attention people pay to its appearance in daily life, only recently has neuroaesthetic inquiry turned its attention to questions concerning the aesthetic appraisal of the human body. We review evidence illustrating that the complexity of aesthetic experience is reflected by dynamic interplay between brain systems involved in reward, perceptual and motor processing, with a focus on aesthetic perception involving the human body. We then evaluate work demonstrating how these systems are modulated by beholders' expertise or familiarity. Finally, we discuss seminal studies revealing the plasticity of behavioural and neural responses to beauty after perceptual and motor training. This research highlights the rich potential for neuroaesthetic inquiry to extend beyond its typical realm of the fine arts to address important questions regarding the relationship between embodiment, aesthetics and performing arts. We conclude by considering some of the criticisms and limitations of neuroaesthetics, and highlight several outstanding issues for future inquiry.

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1. Introduction

Beauty and aesthetics have been the subject of curiosity since antiquity, provoking discourse and debate within philosophy by many of western society's most esteemed thinkers, including Plato, Kant, and Hume (Hume, 1777; Kawabata and Zeki, 2004; Rolls, 2014). The Oxford dictionary defines aesthetics as "a set of principles concerned with the nature and appreciation of beauty" (Oxford Dictionaries online). Beauty frequently (but certainly not always) forms the core of an aesthetic experience, which is thought of as one that delivers gratification of the senses or sensuous delights (Goldman, 2001). While interest in aesthetics has extended beyond the realm of philosophy for at least the past century, it now attracts serious empirical attention from cognitive psychology (*e.g.*, Leder et al., 2004) and neuroscience (*e.g.*, Chatterjee, 2011, 2013). In an attempt to lend a biological perspective to the understanding of aesthetics, Chatterjee and Vartanian (2014) suggest that aesthetic experiences emerge from the interaction between neural systems involved with sensory–motor processes (sensation, perception and motor system), emotion–valuation processes (reward; emotion; wanting and liking), and meaning–knowledge processes (expertise, context and culture; see also Di Dio and Gallese, 2009). Along these same lines, Xenakis et al. (2012) proposed that the basic emotional states of pleasure and pain play a major role in the formation of an individual's aesthetic judgement, an idea backed up by several other authors (Cupchik, 1995; Ginsborg, 2003; Guyer, 2003, 2008; Iseminger, 2003; Kant, 1914; Matravers, 2003). In this context, the scope of neuroaesthetics extends well beyond visual arts to include, for example, performance arts (*e.g.*, dance) and natural stimuli (*e.g.*, human bodies). Since neuroscientists first proposed a place for the brain in empirical aesthetics (Ramachandran and Hirstein, 1999; Zeki, 1999), it has taken less than two decades for neuroaesthetics to establish itself as a serious discipline with an aim to scientifically examine aesthetics from a neurobiological perspective (Chatterjee and Vartanian, 2014; Leder and Nadal, 2014).

Research in neuroaesthetics has been driven in part by the development and increasing availability of human neuroscience approaches that enable in-depth study of cognitive and emotional processes, such as functional magnetic resonance imaging (fMRI), electroencephalographic (EEG) recording, and transcranial magnetic stimulation (TMS). Using these tools, cognitive neuroscientists interested in a broad range of topics, including perception, emotion, attention, and action, are beginning to illustrate how the aesthetic experience is manifest in the human brain. The development, testing and refining of theoretical frameworks to characterize the neurobiological underpinnings of aesthetic experience have reinforced the notion that art appreciation is a complex, multidimensional process. Rather than revealing a static picture of brain areas associated with one of the many components of aesthetic experience, neuroaesthetics is showing that the complexity of aesthetic experience is reflected by the interplay between dynamic brain systems, whose neurofunctional organization may be modulated by different factors associated to objects, subjects and contexts of the aesthetic experience and can undergo rapid, plastic changes when these factors are manipulated. This opens new possibilities for examining how neuroaesthetics research might inform applied disciplines interested in educating and cultivating art appreciation, broadly construed. While a number of previous reviews have attempted to provide a descriptive and interpretative picture of the neural underpinnings of aesthetic experiences (*e.g.*, Brown et al., 2011; Chatterjee and Vartanian, 2014; Di Dio and Gallese, 2009; Nadal et al., 2012), the main aim of this review is to delineate the primary factors that shape and modulate the aesthetic brain, with a particular focus on the role of the human body as the subject or object of aesthetic perception.

This review is organized into three parts. First, after presenting briefly the core neurobiological components supporting aesthetic evaluation of visual stimuli, we provide a focused review of the three core neural systems implicated in aesthetic processing of the human face, body, and movement: brain regions associated with (1) reward processing, (2) visual perception; and (3) motor responses.[1] The next part of the review explores major factors that modulate a perceiver's aesthetic experience such as visual familiarity and motor expertise and then focuses on studies that have implemented active training interventions to examine how experience changes an observer's aesthetic evaluation of static or moving human bodies. The final section turns a critical eye towards several key limitations and challenges for the nascent field of neuroaesthetics, and sets out limitations of the discipline as well as several outstanding questions for future work. Importantly, a overarching aim of the entire review is to highlight contributions from research using the human body (whether still or in motion) as an aesthetic stimulus, an emerging line of inquiry that holds particularly rich opportunities for advancing our understanding of the relationship between art, aesthetics, and the brain.

2. Embodied aesthetics

2.1. Exploring aesthetics within and beyond the fine arts

From the first investigations into the neurobiological response when beholding fine artworks, such as paintings or sculptures, it became clear that neural engagement extended well beyond the occipital lobe and regions of the brain associated with complex visual processing to include areas generally involved in processing the hedonic value of natural as well artistic stimuli (Brown et al., 2011). For example, Kawabata and Zeki (2004) asked participants with no particular experience in art to make aesthetic judgements of paintings by categorizing them as ugly, neutral or beautiful. Regardless of the category of painting being viewed (*e.g.*, abstract, landscape, portrait, still life), the authors found the orbitofrontal cortex to be more engaged when participants perceived paintings rated as beautiful compared to ugly. In a similar vein, Vartanian and Goel (2004) found that while activity in bilateral occipital gyri, left cingulate sulcus, and bilateral fusiform gyri increased with increasing subjective preference attributed to a series of paintings, the activity in right caudate nucleus, a brain region implicated in reward processing, showed a similar pattern. Thus, brain activity appeared to be modulated by the affective value each viewer associated with individual paintings, suggesting a neurobiological response related to the hedonic value of an artistic stimulus. This

[1] The division of core brain systems implicated in the aesthetic processing of the human body is informed by, and resembles to a certain extent, the divisions suggested by Chatterjee and Vartanian (2014) in their 'esthetic triad' model. The arrangement of the current review to focus on reward, visual perception and motor responses represents a more targeted evaluation of three complementary networks involved in aesthetic experiences involving the human body, and we acknowledge the broader explanatory power of Chatterjee and Vartanian's (2014) 'aesthetic triad' in aesthetic experiences more generally construed.

explanation fits well with other research investigating the reward value attributed to a given stimulus. For example, Small et al. (2001) showed modulation of the medial orbitofrontal cortex the more a participant found chocolate pleasant and rewarding (see also Rolls, 2000).

In a seminal meta-analysis of 93 neuroimaging studies of positive-valence aesthetic appraisal spanning four different sensory modalities (vision, audition, olfaction and gustation), Brown et al. (2011) attempted to establish core neurobiological features common across all aesthetic contexts (as opposed to the other major neuroaesthetics meta-analysis, performed by Vartanian and Skov (2014), which focused on visual studies only). They began by broadening the definition of what counts as an aesthetic stimulus. To this end, they suggested that any stimulus evoking positively-valenced emotions made for a definition of an aesthetic stimulus that was more biologically adaptive in scope. In other words, they suggested that exclusively focusing on artworks misses the point that brain systems typically associated with aesthetic appraisal of artworks largely overlap with those that assign valence to all manner of evolutionarily-salient stimuli, such as the attractiveness of a mate or the desirability of a food item. It is also likely that art appraisal has co-opted the same brain circuits used throughout evolution for biologically adaptive decision-making (Brown et al., 2011). Analyses revealed common areas of activation when participants make a positively-valenced decision about a stimulus in the orbitofrontal cortex, the anterior cingulate, the anterior insula and a ventral portion of the basal ganglia, with the anterior insula emerging as the most concordant area of activation across all 93 studies included in the meta-analysis. The authors were somewhat surprised that part of the insula, more commonly associated with negatively-valenced emotions such as disgust, sadness, and pain, emerged most frequently in studies assessing positive valence across four domains. However, it was the anterior-dorsal insula that emerged from the meta-analysis, which is a region most strongly implicated in functional integration of such processes as emotion, empathy, interoception, olfaction and gustation (Kurth et al., 2010). The findings from the meta-analysis led the authors to propose a functional connectivity model of aesthetics whereby appraisal of a stimulus is achieved by comparing subjective awareness of one's current homeostatic state (achieved by the insula) with exteroceptive perception of stimuli in the environment, mediated by sensory pathways that lead to the orbitofrontal cortex. Such a model fits well with the authors' proposal that an aesthetic system first evolved to appraise the valence of objects of biological importance, and is now also used for evaluating artistic works, from songs to paintings.

In this context, it is surprising that only a few neuroscientific studies have investigated the neural correlates of aesthetic appreciation of the form and motion of the human body, a stimulus category that has incomparable biological relevance and has widely been the object and the instrument of art creation. Over the past decade, a richer literature has developed that explores the roles played by reward, visual perception, and the motor system when perceiving and appraising the valence of the appearance and movement of the human body (Fig. 1). These factors are considered in turn, with a particular focus on the emerging theories that attempt to link the empirical findings into a broader framework of neuroaesthetics.

2.2. Reward, emotion and aesthetics of the human body

Initial evidence supporting the activation of reward circuitry in the processing of person attractiveness comes from the study of facial beauty (Hahn and Perrett, 2014; Senior, 2003). In a seminal study, Aharon et al. (2001) were the first to document with behavioural measures a dissociation between facial attractiveness ratings and their reward value. The authors found that male participants rated as more attractive those faces that were judged as more beautiful in an independent pilot study, both when they depicted individuals of the same sex and opposite sex. However, male observers only made an effort to lengthen the exposure of beautiful female faces, but not male faces, in a different behavioural task in which they could control the duration of stimuli through a key press. This finding suggests that beautiful male faces were judged as aesthetically pleasant, but not as rewarding, as female faces. Observing beautiful *vs.* average-looking opposite-sex faces, which were both attractive and rewarding, activated reward circuitry areas, including the nucleus accumbens, orbitofrontal cortex, ventral tegmentum and sublenticular nucleus. Crucially, observing beautiful *vs.* average same-sex faces, which were attractive but not rewarding, also activated the ventral tegmentum but induced a negative response in the nucleus accumbens and sublenticular nucleus. All together, while this pattern of findings points towards a partial dissociation between reward processing and attractiveness ratings, it also suggests that attractiveness may engage some reward circuitry areas independently from sexual desire.

A subsequent study (O'Doherty et al., 2003) investigated neural responses to face attractiveness in heterosexual male and female observers. Observing attractive compared to non-attractive faces, independently from the observer's sex, induced greater activation of the medial orbitofrontal cortex, which was further increased when the faces depicted a positive rather than neutral expression. O'Doherty et al. (2003) concluded that the profile of activity of the orbitofrontal cortex reflects the rewarding value of facial stimuli.

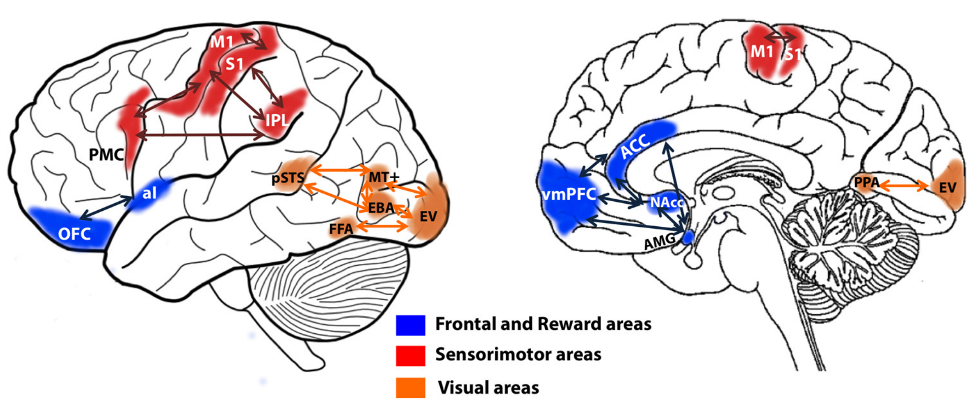

Fig. 1. Schematic representation of the neural circuits implicated in aesthetic judgement tasks. In blue, brain regions associated with reward processing, OFC = orbitofrontal cortices, vmPFC = ventromedian prefrontal cortex, ACC = anterior cingulate, AMG = amygdala; aI = anterior insula, and NAcc = nucleus accumbens; in red, sensorimotor areas, M1 = primary motor area, S1 = primary somatosensory area, IPL = inferior parietal lobule, PMC = premotor cortex; in orange, visual areas, part of the occipitotemporal cortex: EBA = extrastriate body area, MT = motion integration area, EV = early visual area, PPA = parahippocampal place area, and pSTS = posterior superior temporal sulcus. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

In both of these previous studies (Aharon et al., 2001; O'Doherty et al., 2003), participants passively observed pictures of faces. In a later neuroimaging study (Cloutier et al., 2008), male and female observers were explicitly asked to rate the attractiveness of opposite-sex faces while undergoing functional neuroimaging. The results showed that reward circuitry areas, namely the left orbitofrontal and medial prefrontal cortex, the anterior cingulum and bilateral nucleus accumbens, showed a response profile of increasing activity with increasing attractiveness ratings, while the right lateral orbitofrontal cortex and the left medial prefrontal cortex showed the opposite pattern, with increasing activity for decreasing attractiveness ratings. While the activity of reward circuitry areas shows a linear increase with increased attractiveness ratings of faces, the activity of other areas, for example the amygdala, which is involved in processing the valence of different types of emotions, seems to show a non-linear profile of activation, with greater responses to highly attractive and highly unattractive faces compared to average faces (Winston et al., 2007).

The response of frontal areas during explicit attractiveness ratings may not only reflect the intrinsic aesthetic property of a stimulus, but also their general involvement in affective evaluative judgements. In particular, the dorsolateral prefrontal cortex has been shown to be more engaged when people rate the attractiveness of faces compared to other judgements of faces, such as their emotion or colour (Nakamura et al., 1998), identity (Chatterjee et al., 2009), or age (Winston et al., 2007). Together, these findings reflect the specific requirement of an attractiveness judgement as compared to perceptual processing of facial features. In addition, the activity of the anterior dorsolateral prefrontal cortex parametrically increases with increasing attractiveness ratings of faces (Cloutier et al., 2008; Vartanian et al., 2013). The causative involvement of prefrontal areas in the aesthetic evaluation of faces has been documented using transcranial direct current stimulation (tDCS), a brain stimulation technique that can alter cortical excitability by applying weak electric current to the scalp (Ferrari et al., 2015). In this study, Ferrari et al. (2015) found that increasing cortical excitability of the right, but not left, dorsolateral prefrontal cortex increased the perceived attractiveness of faces, independently of their aesthetic and rewarding values before stimulation, but did not alter age estimation.

The impact of attractiveness on brain activity has been documented not only for faces, but also for whole bodies. Platek and Singh (2010) asked male observers to rate the attractiveness of pre- and post-operative pictures of female patients undergoing plastic surgery to adjust waist-to-hip ratio, which is widely considered an index of women's beauty. Results showed greater activation in bilateral orbitofrontal cortex for post-surgical pictures, which were also rated as more attractive, as compared to pre-surgical ones. Furthermore, the activity of these areas, in addition to subcortical structures such as the nucleus accumbens, caudate and putamen, increased with increasing attractiveness ratings. Similar results were obtained in a recent fMRI study in which faces and bodies were presented to female and male observers and neural activity was compared when participants viewed stimuli rated as beautiful or ugly with those rated as neutral (Martín-Loeches et al., 2014). In keeping with previous studies, activity in the nucleus accumbens and anterior cingulate cortex increased with increased attractiveness ratings, with highest response to beautiful pictures and lowest to ugly ones. Other areas, however, in particular the precuneus, posterior and middle cingulate cortex and the medial orbitofrontal cortex, showed a non-linear profile, with higher response to both beautiful and ugly pictures compared to neutral ones. Thus, in line with neuroimaging studies of perceiving artworks (see Section 2.1), the aesthetic experience of perceiving people's faces and bodies relates not only to processing the reward value of their beauty, but is also shown to be a more complex phenomenon involving emotional responses to the salience of extreme ugliness. Accordingly, a recent electrophysiological study (Muñoz and Martín-Loeches, 2015) has shown that a P300 event related potential response, with a mostly frontal distribution, increases when participants view beautiful compared to neutral and ugly bodies and faces, which the authors interpret as reflecting categorization of stimulus valence. However, the late positive complex, with a mostly parietal distribution, was larger for both beautiful *and* ugly stimuli, compared to neutral stimuli. The authors interpret this finding as reflecting increased task demands for judging emotionally salient stimuli, regardless of valence.

In addition to the inherent properties of a face or a body that might be deemed aesthetically pleasing or not, evidence exists to suggest that other factors can also shape the neurobiological foundations supporting aesthetic experience, such as whether an observer is actively engaged in an explicit aesthetic rating task rather than passively observing the stimuli. Di Dio et al. (2007) performed a study that directly compared these two situations by examining brain activity during passive observation or aesthetic rating of Classical and Renaissance sculptures of the human form that either respected or disregarded the golden section in their composition. The golden section is an index of body proportion that is accepted as a normative Western representation of beauty. Results showed that passive observation of the versions of the sculptures that respected *vs.* those that disregarded the golden section induced activation of the right insula and middle prefrontal areas, in addition to bilateral occipital and premotor areas (see below). Conversely, during the explicit aesthetic rating condition, the sculptures judged as beautiful induced a stronger activation of the right amygdala compared to those judged as ugly. The authors concluded that these two patterns of activation reflected, respectively, the processing of the hedonic value of the intrinsic parameters of the stimuli and the subjective emotional reaction to them. All in all, the studies in this section suggest that the activation of the reward system and prefrontal areas during aesthetic experiences of human bodies and faces depends on the intrinsic beauty (or ugliness) of a given stimulus, as well as the observer's mindset or task when viewing the body or face in question.

2.3. Visual perception and aesthetics of the human body

Early neuroaesthetic accounts emphasized a strong connection between the properties of the human visual system and art creation (Zeki, 1999). Indeed, the organization of artworks may meet the basic function of the visual system in the search for constant features of objects, scenes and people. This view was supported by neuroimaging studies of art appreciation that showed modulation of visual areas during observation of paintings depicting abstract forms, landscapes, portraits or still life (Kawabata and Zeki, 2004; Vartanian and Goel, 2004).

In addition to viewing paintings, it was also shown that the preference attributed to natural stimuli, such as faces and bodies, modulated the activation of category selective areas in the medial and lateral occipitotemporal cortex (Yue et al., 2007; Chatterjee et al., 2009; Kedia et al., 2014; Lutz et al., 2013; Marzi and Viggiano, 2010; Ortigue and Bianchi-Demicheli, 2008; Pizzagalli et al., 2002; Trujillo et al., 2013). For example, viewing more attractive faces has been associated with greater activation of the fusiform face area compared to less attractive ones (Chatterjee et al., 2009), thus suggesting that neural activity in these category-selective perceptual areas is influenced by stimulus pleasantness. Crucially, while aesthetic modulation of parietal, prefrontal, insular and cingulate cortices (see Section 2.2) was found only during an explicit aesthetic rating task, modulation of occipitotemporal areas according to the attractiveness of faces was present also during a purely-perceptual gender discrimination task, suggesting that these areas may implicitly code the aesthetic values of perceived stimuli (Chatterjee et al., 2009). Similar aesthetic modulation has also been reported in the extrastriate body area (EBA), a lateral occipitotemporal area that responds selectively to human bodies and body parts (Downing et al., 2001). In a task where participants observed and rated their enjoyment of professional dancers performing ballet and contemporary dance movements, the more participants liked an observed movement, the more EBA was engaged (Cross et al., 2011).

However, modulation of neural activity in perceptual areas according to the aesthetic value of a stimulus does not tell us whether these activations are *necessary* for a rewarding aesthetic experience or are simply epiphenomenal to an observer's aesthetic experience. For example, activity in perceptual areas may be greater for more liked stimuli because participants tend to pay more attention to them (Downing and Peelen, 2011). Testing attractiveness judgements in brain lesion patients and applying trains of repetitive TMS (rTMS) pulses in healthy individuals to disrupt neural processing in the areas beneath the coil are two approaches that hold potential to reveal causal involvement of perceptual areas in aesthetic experience. In one such study, it was shown that prosopagnosic patients with lesions of the fusiform face area not only were impaired in the discrimination of facial identity, as compared to healthy individuals, but they also showed deficits in rating face attractiveness and in attractiveness-motivated behaviour (measured in terms of viewing time; Iaria et al., 2008). Using rTMS in healthy subjects, Calvo-Merino et al. (2010) presented a series of static images of dance postures and asked participants to rate which one of two dance postures they liked more. Results demonstrated that rTMS over EBA blunted aesthetic judgements about body postures relative to rTMS over the ventral premotor cortex. This pattern of findings was relative to aesthetic preferences observed for each participant in a rating session without stimulation. No effect of rTMS over EBA was obtained for the aesthetic judgements of scrambled versions of the same body postures, which shared the same visual features (*e.g.*, colour and contrast) of the originals, but lacked information about the human form.

While the study by Calvo-Merino et al. (2010) showed evidence for causal involvement of EBA in aesthetic appreciation of the human body, it did not allow the authors to test whether aesthetic ratings of bodies changed in a specific direction after interference with EBA. To address this question, a recent study by Cazzato and colleagues (2014) applied rTMS over EBA during judgement of the aesthetic value ("liking") of male and female body stimuli. Importantly, Cazzato et al. (2014) varied the size and implied motion of the bodies in order to modulate their aesthetic value in a predictable direction, with higher aesthetic rating of more dynamic and thinner stimuli (Cazzato et al., 2012). Results showed that, in both male and female observers, rTMS over EBA affected aesthetic ratings only of opposite sex models. However, the direction of the aesthetic rating changes was different according to the sex of the observer and the stimulated hemisphere. Indeed, while stimulation of both left and right EBA decreased the aesthetic ratings of female models in men, in women only rTMS over right EBA affected aesthetic ratings of male models, with an overall increase of aesthetic ratings. These results not only show that neural activity of EBA is necessary for processing those aesthetic properties that are used to appreciate the body of potential sexual mates, but also suggest that the neural organization underpinning the processing of these properties differs between men and women. This result is in keeping with findings of different lateralization of visual body processing in men and women (Aleong and Paus, 2010) and with studies showing sex-related differences in the activation of the left and right hemispheres during aesthetic ratings of paintings and photographs (Cela-Conde et al., 2009). Taken together, the studies reviewed in this section show that modulation of neural activity in visual cortical areas is a crucial component of the neural architecture supporting aesthetic experience, and that differences in the neurocognitive organization of perceptual processing may subserve, at least partially, individual differences in the aesthetic value attributed to environmental stimuli.

2.4. The role of the motor system in aesthetic experience

Since the seminal neuroimaging studies exploring brain regions implicated in aesthetic appreciation (Kawabata and Zeki, 2004; Vartanian and Goel, 2004), it was apparent that, in addition to brain areas associated with reward and visual processing, the motor system was also involved. Kawabata and Zeki (2004), for example, reported that while the orbitofrontal cortex showed increased activity for paintings rated as more pleasant, the motor cortex was more active when participants viewed paintings they rated as ugly, compared to pleasant or neutral. A similar activation of primary sensorimotor cortex was observed by Di Dio et al. (2007) when participants viewed sculptures of the human form rated as ugly *vs*. pleasant. Activation of the motor cortex during aesthetic judgement has been speculated to relate to preparing the observer for action, either to avoid unpleasant (ugly) stimuli or approach a pleasant (beautiful) stimulus (Armory and Dolan, 2002; Kawabata and Zeki, 2004).

The role played by the motor cortex in aesthetic experience has been reconsidered, however, by a theoretical framework proposed by Freedberg and Gallese (2007). According to this framework, the simulation of actions, emotions and corporeal sensations provoked by a particular art form brings about an aesthetic experience. This theory, called the *embodied simulation account of aesthetics*, is largely based on the notion that a tight link exists between perception and action (Prinz, 1997; Schütz-Bosbach and Prinz, 2007) and on experimental findings in both monkeys and humans that action perception engenders activation of the observer's motor system (Rizzolatti and Craighero, 2004). By allowing embodiment of the actions depicted on a canvas or performed by an actor or dancer on stage, or in any other way elicited by an artist via an artistic medium, sensorimotor brain regions contribute to the aesthetic evaluation of a given artwork and underpin a spectator's empathic response towards the art (Ticini et al., 2015).

Evidence supporting the role of sensorimotor embodiment in an individual's aesthetic experience of fine artworks comes from studies showing greater activation of motor and premotor cortices during observation of sculptures or paintings as compared to modified, non-artistic versions of the same stimuli. For example, Battaglia et al. (2011) reported that cortico-spinal excitability measured from a wrist extension muscle was facilitated, thus indexing motor simulation, when participants viewed of Michelangelo's *Expulsion from Paradise* painting (showing a hand extension movement), compared to observing a real hand photographed in the same pose depicted in the painting, or of other paintings showing relaxed or flexed hands (*e.g.*, Michelangelo's *Creation of Adam* or Bellini's *Dead Christ with Angels*). The movement specificity of these findings, which was independent from the emotional intensity of the paintings, further points to the relationship between appreciation of the aesthetic quality of a work and motor mapping of the implied movement within it. In a similar vein, Lutz et al. (2013) used fMRI to compare neural activity during aesthetic ratings of human forms depicted in canvases or in photographs. Results showed greater activation of not only extrastriate, but also posterior parietal cortex to bodies viewed within an artistic context than in natural photographs. Similarly, an EEG experiment by Umilta et al. (2012) found suppression of the mu rhythm (indexing motor activation) during passive observation of Lucio Fontana's slashed canvases (where the action of the artist is not seen, but can readily be inferred), but not during observation of graphically modified versions of them. Thus, evidence from TMS, fMRI, and EEG studies converges to suggest that motor simulation of movements implied in artworks is relevant for their aesthetic appreciation.

In a review paper, Nadal et al. (2012) add further support to Freedberg and Gallese's proposal (2007) by describing the aesthetic experience as one that is fully embodied and enactive, in which an observer's prior experience or expertise plays a role. They note different brain processes involved in positive aesthetic experiences, including: (i) the enhancement of somatosensory cortical processing (Calvo-Merino et al., 2008, 2010); (ii) activation of reward circuits (including cortical and subcortical brain regions) involved in generating pleasant emotions and in evaluating and anticipating an artwork's reward (Kawabata and Zeki, 2004; Vartanian and Goel, 2004); (iii) and attentional modulation of a number of cortical sensory regions that enhance perceptual processing of different features of a perceived artwork (Cela-Conde et al., 2004).

When considering the role of the motor system in an observer's aesthetic experience, research investigating dance has contributed a number of important insights (Cross and Ticini, 2012). Dance is, at its core, a dynamic art form that is open to subjective interpretation by the dancer and the spectator (Bläsing et al., 2012; Orgs et al., 2016). Calvo-Merino et al. (2008) were the first to use human neuroscience tools to investigate brain processes underlying an observer's aesthetic experience of watching dance. They built on previous work using static images or limited body movement by investigating the relationship between activity within sensorimotor cortices when watching dance and aesthetic judgements. Functional MRI scans of non-dancers' brains were recorded while they viewed ballet and capoeira movements that were later rated on a series of aesthetic dimensions (Berlyne, 1974). Calvo-Merino and colleagues reported greater activity in bilateral occipital cortices and in the right premotor cortex while participants watched dance movements they later assigned high liking ratings to (as an average group mean), in comparison to dance movements that received low average liking ratings. The authors concluded that visual and sensorimotor areas play a role in an automatic aesthetic response to dance, in terms of how much spectators enjoy watching a movement.

In an innovative study, Grosbras et al. (2012) combined fMRI with TMS to identify brain areas implicated in emotion processing during dance observation (fMRI) and then test changes to emotional responses induced by temporary reduction of neural activity in the same areas (TMS). They first scanned one group of participants while they watched a 3-min modern dance piece, and later assessed the mean valence of these participants' emotional state throughout the piece using a continuous emotional rating scale. This procedure revealed a significant negative correlation between activity in the posterior parietal cortex and mean emotional valence during dance observation. In a new group of participants, they applied inhibitory rTMS over this area of parietal cortex for 15 min, and then asked these participants to watch the same dance piece while making continuous ratings of their emotional valence. They found that rTMS over right posterior parietal cortex led to enhanced emotional responses (*i.e.*, more positive responses) to dance segments that elicited positive emotions among the previous group of participants (Grosbras et al., 2012). These results were the first to test a link between posterior parietal cortical activity and emotional responses to dance, and raise a number of challenging questions concerning the role of embodiment in dance enjoyment that are addressed in the next section.

3. Shaping and reshaping the aesthetic brain

While most studies of aesthetic processing (including those discussed in this review so far) focus on the perceptual features of a stimulus or on the task performed by an observer, it is important to note that, to a large extent, aesthetic processing is also influenced by an observer's previous experience and knowledge (Kirk et al., 2009; Bohrn et al., 2013). Moreover, these factors can be entirely orthogonal to the perceptual features of a stimulus or the cognitive demands of the task. In this section of our review, we focus on how the aesthetic experience of the human body is shaped by the expertise of the individual experiencing the stimulus, and how it can be modified or changed (by training, for instance). Table 1 summarizes the principal aim and results of the main studies investigating the modulation of behavioural and cognitive correlates of aesthetic experiences according to the beholders' expertise or familiarity (Section 3.1) as well as their plasticity after perceptual (Section 3.2) and motor (Section 3.3) training, focusing on aesthetic experience involving the human body.

3.1. Familiarity and expertise

The notion that familiar stimuli are rated as more pleasant has been widely investigated in the field of face and, more recently, body attractiveness. Indeed, it has been proposed that the perception of stimuli from homogenous classes that share common configurations, such as faces and bodies, is based on the features of a template representation that is used as a reference point to perceive other exemplars, and that those exemplars that are more similar to the template representation receive higher aesthetic appraisals (Valentine et al., 2004). This seems to occur because stimuli that are more similar to a face template, as compared to distinctive faces, are processed more efficiently, as shown both in terms of faster discrimination performance and reduced early perceptual EEG responses (Trujillo et al., 2013).

The relationship between motor expertise and aesthetic experience has been investigated in particular detail within the domain of dance. Cross et al. (2011) sought to quantify the relationship between observers' ability to physically perform a dance movement and how much they liked watching that movement. Participants rated their perceived ability to physically reproduce dance movements performed by professional ballet dancers (after Cross et al., 2006), and assigned each movement an aesthetic rating on the like-dislike dimension of Berlyne (1974). They found that participants tended to like most those movements they perceived as difficult to perform themselves. Furthermore, this interaction between liking and physical ability was represented by stronger activation within occipital and parietal cortices. These results were intriguing, as they suggested that the *less* an observer is able to perform a perceived action, the *more* he or she enjoys watching it (and vice versa). The authors have described this as a 'Cirque du Soleil effect', meaning that we like watching spectacular or impressive movements most of us could never reproduce because of the discrepancy between our bodies/physical repertoires and those of talented dancers, acrobats, or professional athletes (see Cross, 2015, for further discussion of this idea). Returning to Freedberg and Gallese's embodied simulation account of aesthetics, it could be that engagement of sensorimotor areas when observing spectacular or sublime movements that are well beyond an observer's abilities reflects an attempt by the sensorimotor system to embody these impressive movements, or perhaps to assimilate the unusual or complex movements into existing motor codes (*c.f.* Cross et al., 2012).

Recent work by Leder et al. (2012) adds further support to this viewpoint. These authors demonstrated that participants' aesthetic enjoyment of paintings was enhanced by asking them to perform actions that matched an artist's painting style (for example, performing pointillist-style dabbing of paint increased participants' liking of pointillist paintings). Not only executing the actions, but also observing static images depicting the corresponding actions

Table 1
Studies exploring the plasticity of the neurocognitive bases of aesthetic appreciation in long-term experts or after laboratory-induced training experience – with a focus on human body perception.

Authors	Date	Methodology	Stimuli	Population	Primary research question	Major finding
Familiarity and expertise						
Valentine et al.	2004	Behaviour	Photographs of female faces, in full-face and profile view	Non-experts	*Perceptual familiarity* Examine the effect of manipulating the averageness of female faces in profile and full-face views on the perception of attractiveness	Faces morphed towards the average were perceived as more attractive in both views, but the effect was significantly stronger for full-face views.
Trujillo et al.	2013	EEG and behaviour	Attractive, unattractive, and averaged Human and Chimpanzee faces (categorization task)	Non-experts	*Perceptual familiarity* Test of the averageness theory of facial attractiveness by comparing behavioural and ERP responses to high-attractive, averaged, and low-attractive faces presented in the context of a simple species face categorization task.	*Behaviour*: Attractive and averaged faces are more prototypical than unattractive faces. Averaged faces rated as being more attractive *EEG*: High-attractive and mathematically averaged faces both engage fluent facial processing at early stages of visual perception.
Leder et al.	2012	Behaviour/Priming	Paintings (pointillist *vs*. Stroke style)	Non experts	*Motor familiarity* Examine how perceiving a painting style elicits covert simulations of concordant hand movements in the viewer, with and without motor priming.	Participants' aesthetic enjoyment of paintings was enhanced by asking them to perform actions that matched an artist's painting style.
Ticini et al.	2014	Behaviour/Priming	Paintings (pointillist-style)	Non-experts	*Motor familiarity* To what extent is art appreciation dissociable from motor activity and to what extent is it linked to it? Priming with images depicting a motor act either compatible or incompatible with the simulation of the artist's movements (precision *vs*. power grip)	Action priming, when the action is congruent with the artist's painting style, enhanced aesthetic preference.
Cross et al.	2011	fMRI and behaviour (ratings)	Classical ballet/contemporary dance	Non-dancers	*Motor familiarity* How is an observer's aesthetic evaluation of dance related to his or her perceived physical ability to reproduce the watched movements?	*Behaviourally*: Participants reported liking movements more that they perceived as difficult to physically perform. *fMRI*: The interaction between liking and physical ability was represented by greater activity within occipitotemporal (EBA) and parietal brain regions.

Table 1 (*Continued*)

Authors	Date	Methodology	Stimuli	Population	Primary research question	Major finding
Training the aesthetic brain: visual experience						
Hayn-Leichsenring	2013	Perceptual exposure/Behaviour	Human face photographs and art portraits	Non-experts	Investigate effects of adaptation to attractive and unattractive human faces on the perceived attractiveness of human faces in photographs and art portraits	Adaptation to facial attractiveness elicits after-effects in the perception of subsequently presented faces for both face photographs and art portraits. These effects did not cross image domains (*i.e.*, between photographs and portraits).
Rhodes et al.	2003	Perceptual exposure/Behaviour	Faces images	Non-experts	Examine the effect of brief exposure to consistent facial distortions on what looks normal (average) and what looks attractive	Perceptual adaptation can rapidly recalibrate people's preferences to fit the faces they see.
Mele et al.	2013	Perceptual exposure/Behaviour	Body images	Non-experts	Investigate how perceptual experience modulates body aesthetic appreciation.	Found a tendency for participants to consider more attractive those bodies whose weight is similar to that of previously encountered bodies.
Winkler and Rhodes	2005	Perceptual exposure/Behaviour	Body images	Non-experts	Investigate whether short durations (5 min) of exposure to distorted bodies can change subsequent perceptions of attractiveness and normality.	Perception of body attractiveness can be influenced by experience, but there is an asymmetry between the effects of exposure to narrow and wide bodies. The most attractive body shape was consistently narrower than the most normal looking body shape.
Orgs et al.	2013	Sequence exposure/Behaviour	Apparent motion with static body postures	Non-dancers	Investigate the aesthetic effects of three levels of movement representation: body postures, movement transitions and choreographic structure; with different kinds of priming.	Participants exposed to asymmetrical sequences showed increased liking of asymmetrical sequences. Moreover, participants preferred movements that had been frequently observed to movements that were seen less frequently.
Training the aesthetic brain: motor experience						
Kirsch et al.	2013	Training/Behaviour	Street dance sequences	Non-dancers	Clarify the relationship between physical experience and affective evaluation of dance movements. In a between-subjects design, participants received either physical, audiovisual or auditory only training.	Participants from the physical training group not only improved their physical performance of the dance sequences, but also reported higher enjoyment and interest in the dance sequences after training.
Kirsch et al.	2015	fMRI pre- and post-training	Street dance sequences	Non-dancers	Investigate how learning to perform an action impacts the neural response when watching and aesthetically evaluating the same action. In a within-subjects design, participants received physical, audiovisual and audio only training on different dance sequences.	After experience, brain regions involved in mediating the aesthetic response shifted from subcortical regions associated with dopaminergic reward processing to posterior temporal regions involved in processing multisensory integration, emotion and biological motion.

increased the participants' aesthetic enjoyment of paintings, after the participants received a visuo-motor training to associate each specific action to the corresponding painting style (Ticini et al., 2014). These findings fit nicely with Freedberg and Gallese's embodied simulation account of aesthetics (2007), showing that the more an observer can simulate the painter's movements in producing art, the more he or she reports liking the artwork.

3.2. Training the aesthetic brain: visual experience

As explored in the previous section, an observer's familiarity or expertise with a stimulus can profoundly shape how it the stimulus in question is perceived and evaluated. Here we review studies that have actively manipulated these factors and document the plasticity of the visual, motor and reward systems during aesthetic appreciation.

Considering perceptual familiarity, it is known that the norm-based representations used to perceive face and body stimuli may be shaped by experience, since the template corresponds to the average of all exemplars that have been previously encountered by a given individual. Importantly, pre-exposing observers with repeated presentations of photographs or portraits of faces increases aesthetic ratings compared to novel face stimuli (Hayn-Leichsenring et al., 2013; Rhodes et al., 2003). Similar results have been obtained for the aesthetic appreciation of body shape, with a tendency to consider more attractive those bodies whose weight is similar to that of previously encountered bodies (Mele et al., 2013; Winkler and Rhodes, 2005). Of note, the effects of body weight familiarization correlate with the degree of body dissatisfaction and internalization of Western ideals reported by participants (Glauert et al., 2009). This suggests that perceptual familiarity with the type of extremely thin models featured by the media may explain the tendency to idealize lean body shapes, which is particularly strong in Western societies.

Perceptual familiarity may affect not only the aesthetic value attributed to the form of bodies, but also how we appreciate their movements. Findings by Orgs et al. (2013) further support the relationship between familiarity and liking. In this study, the authors found that participants preferred movements that had been frequently observed to movements that were seen less frequently (Orgs et al., 2013). By using apparent biological motion where still photographs of a dancer in different poses were presented in rapid succession, and pre-exposing participants to either symmetrical or asymmetrical movement sequences, Orgs and colleagues found that participants exposed to asymmetrical sequences showed increased liking of asymmetrical sequences. It is of note, however, that pre-exposing participants to symmetrical sequences did not affect later ratings. The authors take this as evidence of a "baseline" preference for sequential symmetry that does not depend on familiarization in the exposure phase.

While the studies discussed in this section demonstrate that acquiring perceptual familiarity affects aesthetic appreciation of face and body stimuli, to our best knowledge, little is known on the neural underpinning of these modifications. In contrast, the following section focuses more on the effects of acquiring direct motor experience with performing arts, and explores the effects of this training on both behavioural and neural indexes of aesthetic appreciation.

3.3. Training the aesthetic brain: motor experience

In addition to acquiring visual familiarity, acquiring direct motor experience with performing or creating art can also change the aesthetic appreciation of others' performances. In the domain of the neuroaesthetics of dance, Kirsch et al. (2013) conducted a between-groups training study with non-dancers to clarify the relationship between physical experience and affective evaluation of dance movements. One group of participants received physical dance training using an immersive video game system, another group received visual and auditory experience with the same dance sequences, and a third group received auditory experience only (*i.e.*, simply listened to the soundtracks that accompanied the dance movements experienced by the other groups). Participants' aesthetic preferences for dance stimuli were measured before and after the training sessions. Results showed that participants from the physical training group not only improved their physical performance of the dance sequences, but also reported higher enjoyment and interest in the dance sequences after training. These data thus suggest that mastering physical performance of movements leads to greater enjoyment while observing them. As well as providing support for Freedberg and Gallese's embodied theory of aesthetics (2007), this finding also resonates with Montero's (2012) suggestion that dance training can facilitate a kinesthetic experience when watching dance, without which some aesthetic aspects of dance performance, such as grace, power, or precision, may go unnoticed among novice observers. As such, Montero suggests that (dance) expertise can facilitate a more differentiated and informed aesthetic experience of a dance performance.

In terms of how these findings compare to the previous study by Cross and colleagues (2011), which found greater enjoyment for movements participants rated as difficult or impossible to reproduce, it appears that when physical experience is experimentally manipulated, and embodiment directly measured (in terms of actual motor performance), the data provide clear support for an embodied simulation account of aesthetics (Freedberg and Gallese, 2007). In a follow-up study aiming to characterize the neural architecture supporting the relationship between training experience and liking, Kirsch et al. (2015) directly compared how learning to perform an action impacts the neural response when watching and aesthetically evaluating the same action. Functional MRI was obtained prior to and immediately following the training period, as were affective and physical ability ratings for each dance stimulus. The authors found that, after training, brain regions involved in mediating the aesthetic response shifted from subcortical regions associated with dopaminergic reward processing to posterior temporal regions implicated in multisensory integration, emotion and biological motion. While this study provides a more in-depth look into the complex and dynamic relationship between experience, aesthetics, reward, and emotion, it also raises many questions regarding the malleability of a perceiver's aesthetic experience, which will require careful further investigation. Moreover, characterizing the shift in processing from brain regions mediating reward to those involved in higher-level perceptual and emotion processing remains an open challenge for future research, in dance and other domains of neuroaesthetics.

4. Challenges and emerging prospects for the future of neuroaesthetics

Our aim for this review has been to contribute a new perspective to the rich body of neuroaesthetics literature by focusing on factors that modulate and shape an individual's aesthetic appraisal of body-related stimuli at brain and behavioural levels. As with any emerging field that combines elements from distinct and arguably distant disciplines (such as neuroscience and art, in this case), it is important to not only evaluate and synthesize the extant research, but also to critically examine the limitations and shortcomings of the field as a whole. In this final section, we attempt to articulate some of these limitations, areas of caution, and pitfalls for this field as ever more researchers undertake empirical investigation of the neurobiological antecedents and consequences of aesthetic experience.

4.1. Maintaining integrity as a line of inquiry in an era of neuromania

While enthusiasm for neuroscience-based approaches to the study of aesthetics continues to grow, the nascent field of neuroaesthetics is also experiencing its share of growing pains. Perhaps unsurprisingly, concomitant with an increasing interest in neuroaesthetics has been a mounting "counter-neuroaesthetics" movement criticizing the use of brain-based approaches to address aesthetic questions (*e.g.*, Ball, 2013; Conway and Rehding, 2013). As Conway and Redhing state, "it is an open question whether an analysis of artworks, no matter how celebrated, will yield universal principles of beauty" (pp. 3), and that "rational reductionist approaches to the neural basis for beauty (...) may well distill out the very thing one wants to understand" (pp. 4, Conway and Rehding, 2013). These authors also criticize many researchers working in the domain of neuroaesthetics for conflating notions of beauty, art and perception, and strongly caution against looking to any one region of the brain as a universal "beauty centre". As they rightly point out, and as the myriad studies discussed in this review illustrate, such a complex reaction (considering a percept to be beautiful) engages a complex pattern of cortical and subcortical activity and can vary based on a number of factors, including many of those discussed in this review, such as the context, expectations and expertise of the beholder.

We agree with Conway and Rehding (2013) that the "neuromania" that threatens to downgrade the legitimacy of neuroathestics is a concern, but also argue that the discipline, at its core, appreciates the intersubjectivity of individuals' aesthetic experiences, and is not seeking to establish universal absolutes about the neurobiology of beauty. However, along with the concerns raised by Conway and Rehding (2013), a number of other issues require careful consideration as this nascent discipline matures, which we consider in the following section.

4.2. Mapping the neurobiological substrates of aesthetics: to what end?

One important challenge for the field concerns the extent to which universal neural substrates supporting the experience of beauty should even be sought, when interindividual differences might be more interesting and illuminating than what is common across individuals. We presented several studies that have begun to scratch the surface on the impact of task demands (Di Dio et al., 2007; Chatterjee et al., 2009), expertise (Bohrn et al., 2013; Kirsch et al., 2013, 2015; Orgs et al., 2013; Ticini et al., 2014), visual familiarity (Mele et al., 2013; Rhodes et al., 2003; Winkler and Rhodes, 2005), and the observer's sex (Cazzato et al., 2014; Cela-Conde et al., 2009), but myriad additional factors could influence an observer's aesthetic preference and response, including culture, age, and education level, to name a few. As the field is still so young, not enough data exist to create a clear or complete picture of what influences or drives perceptions of beauty. We anticipate that in the years ahead, the field of neuroaesthetics will continue to grow, and will begin to provide answers to some of these questions. As long as scientists engaged in the pursuit of characterizing the biological foundations of aesthetics respect the limits of human neuroscientific approaches, we foresee a bright future in the study of neuroaesthetics.

4.3. Disentangling aesthetics from emotion

Another frequently mentioned criticism of a common neuroaesthetics approach is the subjectivity of liking ratings assigned to stimuli (Heller et al., 2011; Kahneman and Klein, 2009). By relying on extremely simplistic ratings of liking (often just 'like *vs.* dislike'; *c.f.* Zeki et al., 2014), it does not seem feasible (or sensible) to attempt to characterize a common neural architecture supporting the human perception of a beautiful or aesthetically pleasing stimulus. One way to overcome, or at least begin to address, this concern would be to consider a positive evaluation of a stimulus more as a feeling, such as a positively-valenced emotion. Methods used for subtle emotion detection, such as facial EMG (Dimberg et al., 2000) and galvanic skin response measures, are proving useful for gaining insights into more direct indices of a positive affective experience when beholding a stimulus for aesthetic appraisal (Christensen et al., 2014; Gerger et al., 2014; Leder et al., 2014). We suggest that future experiments could attempt to integrate such implicit measures of aesthetic appraisal with brain imaging measures, such as fMRI or EEG, to gain clearer insights into subtle differences in a perceiver's affective experiences and supporting neural processes.

This, however, raises an important issue for future research in neuroaesthetics: disentangling aesthetic experience from emotion. As discussed in Section 2, many of the neural underpinnings of aesthetic experience in perceptual, motor and reward systems are involved to some extent in both aesthetic experiences and favourable attitudes towards positively valenced stimuli in general, even when they are void of any overt aesthetic value (such as a chocolate bar). In a similar vein, a complex of cortical and subcortical structures has been associated with processing bodily expression of emotions, which partially overlap those involved in body aesthetics (Candidi and Aglioti, 2015; Candidi et al., 2011; de Gelder, 2009; de Gelder et al., 2011, 2010). Furthermore, the direct relationship between emotion and aesthetics has been documented by the finding that activating negative compared to positive emotions and neutral states changes the aesthetic value attributed to both abstract forms and body postures (Era et al., 2015). Which aspects distinguish the patterns of activation within these areas during specifically aesthetic experiences from more general positive affective reactions? One possible working hypothesis relies on the segregation, at least in the rodent brain (Berridge et al., 2009), of two different pathways in the ventral striatum, a crucial component of the reward system. One pathway is mediated by opiate and cannabinoid systems and associated with "liking" experiences, and the other is mediated by a dopamine neurotransmitter system and associated with outcome-related "wanting" experiences. Chatterjee and Vartanian (2014) have proposed that aesthetic experiences rely on the first system in the absence of activity in the second, thus triggering appreciation of object properties independently from a desire to possess or act on the object itself (Ortony et al., 1990). In this view, modulation of neural activity in reward, perceptual and motor areas during aesthetic experience and positive attitudes to stimuli may not so much be segregated in their neuroanatomical organization, but rather in their temporal dynamics and ultimate outcome. For example, while the ultimate consequence of an affective appraisal of a stimulus may be to approach positive stimuli and avoid negative ones (as reflected by the greater activation of primary motor cortex during observation of ugly than neutral and pleasant stimuli; Kawabata and Zeki, 2004; Di Dio et al., 2007), the ultimate product of aesthetic experience may be stimulus perception itself, as reflected by greater activation for pleasant than neutral and unpleasant stimuli in areas involved in perceptual processing and embodiment (*e.g.*, Calvo-Merino et al., 2008; Cross et al., 2011; Di Dio et al., 2007). This may explain why dysfunctions of category-selective extrastriate areas after brain lesion or rTMS interfere with both perceptual and aesthetic processing (Calvo-Merino et al., 2010; Iaria et al., 2008; Urgesi et al., 2007), while processing of emotional information is relatively preserved (Moro et al., 2012).

Although speculative, this hypothesis may be tested by comparing the temporal dynamics and causative involvement of reward, perceptual and motor areas in aesthetic and positive affective experiences.

5. Summary and conclusions

In this review, we have examined the primary factors that influence aesthetic experience in the human brain, focusing on the human body and the role played by embodiment. As a number of other reviews provide detailed description and interpretation of the neural correlates of aesthetic experiences *per se*, here we have instead focused on the plasticity and malleability of an individual's aesthetic experience, with particular emphasis on studies that have examined perception of stimuli involving the human body. While continued in-depth investigation of the neural substrates supporting positive aesthetic experiences of classical paintings and abstract art will undoubtedly further advance understanding of how the human brain supports evaluation and appreciation of art, a widening of focus to include aesthetic evaluation of stimuli that come from domains beyond the visual fine arts, such as dance, or more broadly, body perception, holds promise for generating a more holistic understanding of aesthetics. As highlighted in this review, research in the developing domain of neuroaesthetics is still raising more questions than it is answering, and ongoing and future work will help to construct a more detailed and nuanced picture of the features that shape aesthetic preferences from a neurobiological perspective.

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