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The neural foundations of aesthetic appreciation

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ABSTRACT

The study of the cognitive and neural underpinnings of aesthetic appreciation by means of neuroimaging techniques has yielded a wealth of fascinating information. Although the results of these studies have been somewhat divergent, here we provide an integrative view of the early approaches, which identified some of the core mechanisms involved in aesthetic preference. Then, a number of more specific issues under the perspective of recent work are addressed. Finally, we propose a framework to accommodate these findings and we explore future prospects for the emerging field of neuroaesthetics.

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1. Introduction

Objects created by visual artists, such as oil paintings, sculptures, etchings, drawings, watercolors and even glossies and decorative arts and crafts, constitute remarkable physical expressions of the human capacity to produce and appreciate beauty. All human cultures have studied, discussed and engaged in these activities, though most often from a humanistic, subjective and descriptive perspective. Neuroscientists and neuropsychologists have recently approached the traditionally philosophical field

Abbreviations: BA, brodmann area; DOC, dorsal occipital cortex; EEG, electroencephalography; FG, fusiform gyrus; fMRI, functional magnetic resonance imaging; IOG, inferior occipital gyrus; IPS, intraparietal sulcus; MEG, magnetoencephalography; PFC, prefrontal cortex; TPJ, temporoparietal junction.

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of aesthetics aiming to characterize the neural and evolutionary foundations of our species' capacity to appreciate beauty and art. This approach, known as neuroaesthetics, has begun to provide some insights into the neurobiological bases of aesthetic appreciation (Chatterjee, 2011; Dissanayake, 1992; Jacobsen, 2010; Miller, 2000, 2001; Nadal and Pearce, in press; Ramachandran and Hirstein, 1999; Skov and Vartanian, 2009; Zeki, 1999a,b).

Until recently, researchers could only empirically study the biological mechanisms underlying artistic and aesthetic appreciation and creation by examining single cases of patients suffering from brain lesions or neurodegenerative diseases. Despite their great inherent interest, such accounts were often anecdotal and difficult to understand in the absence of an adequate theoretical framework. Chatterjee (2011) refers to them as "informative anecdotes" (Chatterjee, 2011, p. 54). Meaningful conclusions regarding the impact of different neurological conditions on artistic and aesthetic activities have only emerged after the cases have been gathered and analyzed together by Bäzner and Hennerici (2006), Bogousslavsky (2005), Chatterjee (2004a, 2006), Miller and Hou (2004) and Zaidel (2005, 2010). The main conclusions derived form these analyses merit examination before we turn to neuroimaging studies.

General observations. Despite their proficient visuo-motor and musical skills, artists are vulnerable to the same visual, motor, auditory and cognitive neuropsychological deficits that affect other people. The difference, in Chatterjee's (2004a) words, is that artists manifest these deficits in strikingly eloquent ways. Most of the studied artists continued to be artistically motivated, productive and expressive after the onset of their condition. Personal style is usually preserved to a certain extent, probably due to the years devoted to practicing their skills (Zaidel, 2005). There is no direct relation between suffering from neuropsychological conditions and improvised quality of art production. Chatterjee (2004a) notes several instances in which the effects of the condition on the artworks were aesthetically surprising and pleasing.

The effect of strokes on artistic production. There is a noticeable change in the work of most artists who have suffered a stroke. Many of them resume their creations, though only after overcoming various forms of disability. Some of these artists had to change from working with their dominant to their non-dominant hand (Bäzner and Hennerici, 2006). Although lesions in either hemisphere seem to leave traces on the production of artists (Zaidel, 2005), spatial disorganization (perspective, third dimension, contours), neglect and distortion in facial representation are more obvious in the artworks of artists who suffered a right hemisphere stroke (Bäzner and Hennerici, 2006).

The impact of visual agnosia. The specific effect of visual agnosia on artists' creations depends to a large extent on whether object recognition problems are related with their perceptual or conceptual features (Chatterjee, 2004a). In the first case, artists will often not render the overall form and composition of the depicted objects, but will include some of their conspicuous features. In the latter case, artists are still adept at drawing when copying, but seem completely incapable when asked to draw from memory, and have to rely on their knowledge of the world.

The impact of aphasia. Bäzner and Hennerici (2006) argue that there is little evidence indicating a significant impact of aphasia on the creation of visual art, which suggests that verbal and visual production may be related with distinct output channels. However, Bogousslavsky (2005) and Chatterjee's (2004a) revisions reveal that whereas the production of some aphasic artists seems to be largely unaffected, other artists become more expressive, and yet others begin producing works with different contents, suggesting that this condition may be to broad as a window into the biological bases of artistic and aesthetic production.

The impact of degenerative diseases. Artists suffering from Alzheimer's disease seem to gradually lose the ability to represent the world with precision, but are able to make use of color and form in aesthetically appealing ways (Miller and Hou, 2004). Chatterjee (2004a) notes that the production of these artists continues only as part of the general routines that the artists performed throughout their lifetimes, and only if others around them provide the necessary setting to do so. Some patients with a specific form of frontotemporal dementia, known as semantic dementia, which involves neural degeneration in the left anterior temporal lobe, exhibit new interest in art. These patients approach their pictorial activity compulsively, in spontaneous spouts of creative production, often painting repetitive motifs, leading to progressive improvements to their painting. These depictions are usually realistic, lacking in symbolism or abstract elements (Miller and Hou, 2004).

Other neurological conditions. Epilepsy and migraine have been found to increase the variety of visual elements available to artists who suffer from these conditions, as well as a source of inspiration to them (Chatterjee, 2004a).

These observations reveal that neurological conditions can have diverse –and maybe even distinctive– effects on artistic production. But what about their influence on the other side of the artistic coin –appreciation? What can similar cases tell us about the biological underpinnings of aesthetic appreciation? Given the very few studies that have been carried out on this issue, and their anecdotal nature, we cannot offer a comprehensive response. At present we can only provide a tentative and provisional picture.

The effect of strokes on artistic appreciation. Griffiths et al. (2004) describe a patient who suffered an infarct that left him unable to experience emotion in response to music. The lesion mainly affected the left insula, but extended into the left frontal cortex and amygdala. Speech, which was also initially affected, was recovered after 12 months. However, even though his perception of diverse musical features was normal, 18 months after the stroke the patient was still emotionally unaffected by music, despite the fact that during that time he was able to enjoy other activities. These observations led the authors to suggest that perceptual and emotional components of music processing might rest on functionally and anatomically distinct neural networks, and that the insula is a crucial piece in the neural underpinnings of the emotional response to music.

The impact of degenerative diseases. Halpern et al. (2008) found that artistically untrained patients with Alzheimer's disease were consistent in their preference for visual art on repeated presentations, despite being unable to remember they had seen the art on previous occasions. It seems, thus, that the neurodegeneration that causes Alzheimer's disease does not prevent these patients from expressing aesthetic preference, and that their preferences are as stable over time as those of healthy people. Two reports of patients with frontotemporal dementia describe how their preferences for music changed remarkably (Boeve and Geda, 2001; Geroldi et al., 2000). These three patients began compulsively listening to music they had not previously enjoyed, playing it for hours on end.

Other neurological conditions. Sellal et al. (2003) present a case of an epilepsy patient who underwent left temporal lobe resection, which only spared the hippocampus, the parahippocampal gyrus, and the amygdala. This case is interesting because the surgically removed brain region corresponds roughly to that which typically degenerates in the form of frontotemporal dementia mentioned above. During the first year after surgery the patient became aware that he no longer enjoyed listening to rock music, and that he now preferred Celtic or Corsican polyphonic singing. His taste in literature also shifted, in this case from science fiction to Kafkian-inspired novels. The authors report that the patient also began showing increased preference for realistic paintings, enjoying the small details that previously went unnoticed to him. These changes in aesthetic preference are in contrast with his unchanged preferences for food, fashion or faces.

Damage to the amygdala. The crucial role of subcortical brain structures related with emotional processing in aesthetic appreciation was revealed by two studies of the effects of damage to the amygdala. Adolphs and Tranel (1999) report that there were differences between the preferences for visual stimuli of two patients with bilateral amygdala damage and a group of healthy controls. Both patients expressed higher liking for three-dimensional geometrical shapes, landscapes and color arrangements than the control participants. This difference was especially clear for the stimuli least liked by controls. Similar results were obtained from the examination of musical preferences in a patient with almost exclusive bilateral damage to the amygdala (Gosselin et al., 2007). In this case, whereas the patient was able to correctly process musical features, even tempo and mode, she showed selective impairment in the recognition of scary and sad music, but not of happy music. Thus, it seems that the amygdala plays a role in the affective processes underlying aesthetic preference, especially in the experience of disliking and in relation to negatively valenced stimuli.

The advent and refinement of non-invasive neuroimaging techniques has allowed researchers to build upon these informative cases, and to address similar and new issues in healthy subjects in controlled situations, and to correlate appreciation and enjoyment of music, painting, architecture or sculpture, among other forms of art, with the activity of several brain structures. In the present review we first examine the psychological processes related to the visual appreciation of aesthetics and then bring together the results of early neuroimaging studies and provide an integrative framework of the underlying neural and cognitive foundations. We then show how the most recent neuroimaging approaches have addressed certain specific issues and examine how their results fit within this general framework. Finally, we point out some of the most relevant and challenging questions that arise when this framework is viewed from a broader perspective. In this review we will only be concerned with the appreciation of visual art, though many forms of human artistic production, such as music, literature, theatre, opera, and cinematography, share important aspects with the visual arts.

2. Neuroimaging techniques reach to the arts

In 2004, several neuroimaging studies began constructing the basic picture of the neural correlates of visual aesthetic appreciation (Cela-Conde et al., 2004; Kawabata and Zeki, 2004; Vartanian and Goel, 2004). Another paper on the same topic soon followed (Jacobsen et al., 2006). Due to the fact that these experiments were designed independently, they employed different research strategies and protocols. Thus, it is not surprising that the results obtained were quite disparate (for an account about how these differences might have affected results, see Nadal et al., 2008).

The relation between cognitive and neural processes involved in aesthetic appreciation is highly complex and intricate. The activity of neural networks connecting diverse areas is still crucial for the simplest cognitive processes. Even leaving aside the more philosophical issue of "qualia", i.e., the intimate, personal experience of perception, the issue is formidably complex. The biological foundations of conscious experience seem to involve coordinated firing between groups of neurons belonging to several different, and often distant, areas. This notion was already advocated by early scientific approaches to consciousness (Crick and Koch, 1990; Von der Malsburg, 1981; Cela-Conde and Marty, 1997), and it is still defended today (Shulman et al., 2009).

Thus, it seems that a focus on selected aspects of aesthetic appreciation cannot do justice to the whole panorama of what constitutes the appreciation of beauty by the mind/brain. Explaining such appreciation requires at least a three-step strategy:

(I) An account of the brain regions and neural networks that are related with each phenomenon studied experimentally.
(II) An explanation of the diverse psychological aspects involved in the perceptual/appreciative tasks performed by participants.
(III) A general, integrative model of the cognitive tasks performed, that may eventually explain the qualitative aspects related with those cognitive tasks.

Here, we will try to offer a preliminary approach to such a strategy. We will start with the four 2004–2006 initial studies, providing a synthetic account of what they revealed about the visual appreciation of beauty. Thereafter, we will refer to later experiments that have addressed certain outstanding matters related with aesthetic appreciation. Finally, we will try to assess how cognitive models of the appreciation of beauty fit this set of results.

The focus of our analysis will be on the aesthetic experience, insofar as it encompasses the concept of "beauty". This constitutes a narrow realm in modern aesthetics. Aesthetic qualities refer to judgments derived from sensory contemplation of phenomena and, especially around the 18th century, the concept of beauty is intricately linked to theories of aesthetics. However, in many modern art forms, such as conceptual art, the prime role of beauty has diminished, and is even actively challenged. Thus, an ugly object may still be a great work of art.

2.1. Psychological processes related with the visual appreciation of aesthetics

Ever since Berlyne's (1971, 1974) work, it has been known that aesthetic appreciation rests on diverse psychological processes. Pleasure, expectation, surprise, recognition and interest, to mention but a few of these, undoubtedly play a role in the appreciation of beauty. Contextual features also seem to influence spectators' responses. Additionally, participants' particularities, including social, historical, cultural, biological, educational, and personality variables, are also known to shape aesthetic experiences. Variables related with attention to the stimulus, the motivation to attend and evaluate the stimulus, the emotional response to the stimulus and its rewarding properties contribute to the prioritization and selection of all information, including visual stimulation (Raymond and Narayanan, 2009).

Researchers interested in the biological underpinnings of aesthetic experiences are faced with the problem of dealing with its complex and multifaceted nature. Can neuroimaging techniques adequately deal with the interplay of such varied cognitive, affective, personal, social and cultural factors? The straightforward answer is that their strong methodological restrictions do not allow the observation of brain activity reflecting the whole set of processes involved in aesthetic appreciation. As noted by Chatterjee (2011), researchers have responded to this challenge by studying the neural bases of only few specific aspects or components of aesthetic appreciation at a time. This is done under the tacit –as well as untested– assumption that a reasonably good understanding of the whole aesthetic experience can be gained from the sum of its parts.

One favored option has been to study the isolated effects of certain variables, such as expertise (Berkowitz and Ansari, 2010;

Kirk et al., 2009a; Müller et al., 2009) or context (Kirk et al., 2009b). But inevitably, neuroimaging methods impose serious restrictions on the tasks that participants can be required to perform. Experimenters design such tasks guided by two constraints: the specific research hypothesis and the desire to capture meaningful aspects of their participants' aesthetic experience. By far, the most common task participants have been asked to perform in these kinds of neuroimaging experiments is rating specific features of the stimuli or certain aspect of their experience. This practical strategy necessarily involves losing a considerable amount of information about many other non-measured aspects of the experience. So the choice of task is crucial.

A possible solution to this dilemma is provided by Eysenck's (1940) general factor of aesthetic preference. The fact that this general factor was found to correlate with the ranks awarded to odoriferous substances, several colors and a variety of polygonal figures, led him to surmise that it was directly constrained by the properties of the nervous system. Crucially for the requirements of neuroimaging studies, he believed that, with regards to visual stimuli, this factor accounted for people's appreciation of their beauty (Eysenck, 1940). Several subsequent studies have found support for the notion that beauty ratings capture the aesthetic experience in a more meaningful way than ratings of, for instance, originality, interest, or pleasingness (Pickford, 1955; Looft and Baranowski, 1971; Seifert, 1992; Cupchik et al., 1992; Marty et al., 2003; Jacobsen et al., 2004).

This is not to say that rating the beauty of visual or auditory stimuli, as is required from participants in many neuroimaging studies, rests on a simple single cognitive process. On the contrary, any model of the cognitive processes involved in the appreciation of beauty must also account for multiple factors, such as meaning and recognition, decision judgments, affective processes (pleasure, disgust), and reward. These factors multiply the complexity of visual aesthetic appreciation. In contrast, the experience of beauty seems to be, introspectively speaking, something quite simple – either we find an object to be more or less beautiful, or we find it indifferent. Nonetheless, the complexity of the structure of aesthetic appreciation and the relative simplicity of its manifestation do not collide head on. Since the timescale of the brain's functional activity is in the order of milliseconds, complex processes take place very quickly, leading to a qualitative, simple subjective conclusion about the beauty of a stimulus. How to understand such almost instantaneous complexity should be the objective of any model of aesthetic appreciation.

2.2. Neural activity identified by the early neuroimaging studies

Four initial neuroimaging studies (Vartanian and Goel, 2004; Kawabata and Zeki, 2004; Cela-Conde et al., 2004; Jacobsen et al., 2006) intended to identify the neural correlates of aesthetic appreciation of visual stimuli. Three of them (Cela-Conde et al., 2004; Kawabata and Zeki, 2004; Vartanian and Goel, 2004) registered participants' brain activity while they expressed their preference for visual stimuli or rated their beauty. Their main aim was to compare activity associated with stimuli appraised positively and negatively by each individual participant. The fourth study (Jacobsen et al., 2006) addressed a slightly different issue, asking participants to rate the beauty and symmetry of simple visual stimuli, namely, black and white geometric patterns created by the authors. This study compared neural activity while participants rated the beauty of images with activity while they rated their symmetry. Thus, the results obtained concerning beauty refer to the neural correlates of the judgment of beauty *per se*. It is important to note that all these researchers considered that a subjective rating by the participants themselves was essential, given that it is likely that no general condition of "beauty" exists.

The neuroimaging results could be summarized as follows:

(i) Kawabata and Zeki (2004) registered participants' brain activity with fMRI (functional magnetic resonance imaging) while they rated the beauty of stimuli. They found that activity was greater:
   - in the orbitofrontal cortex for stimuli classified as beautiful;
   - in the motor cortex for stimuli classified as ugly.

(ii) By means of magnetoencephalography (MEG), Cela-Conde et al. (2004) identified activity in the left dorsolateral prefrontal cortex. This activity was especially significant when participants judged stimuli as beautiful, as compared to being non-beautiful, between 400 and 1000 ms after stimuli onset.

(iii) By means of fMRI, Vartanian and Goel (2004) found a double correlation:
   - activity in the right caudate nucleus decreased as preference ratings for stimuli decreased;
   - activity in the left anterior cingulate gyrus and bilateral occipital gyri, increased with preference ratings.

(iv) Although, as we have already pointed out, Jacobsen et al.'s (2006) study differed from the previous three, they did identify some differences when comparing brain activity related with stimuli rated as beautiful and ugly, especially in the frontomedian and anterior cingulate cortex.

2.3. Models of cognitive processes underlying visual aesthetic preference

Chatterjee's (2004b) theoretical model of the cognitive and affective processes involved in visual aesthetic preference, based on visual neuroscience, provides a means to organize the results obtained in the 2004–2006 neuroimaging studies within a series of information-processing phases. The model posits the following stages:

1. The elementary visual attributes of an artwork are processed like any other visual object's (primary and secondary visual brain areas).
2. Attentional processes redirect information processing to prominent visual properties, such as color, shape, and composition (frontal–parietal networks).
3. Attentional networks modulate processing within the ventral visual stream that leads to attributional networks – the "what pathway", i.e., experience of the stimulus, attributes and contents, such as faces and landscapes (temporal lobe).
4. Feed-back/feed-forward processes linking attentional and attributional circuits that enhance the experience of the visual object.
5. Emotional systems intervene in most cases (anterior medial temporal lobe, medial and orbitofrontal cortices, and subcortical structures) (Chatterjee, 2004b).

Jacobsen and Höfel's (2003) proposal offers a complementary view of the general cognitive processes involved in aesthetic appreciation. On the grounds of several electroencephalographic (EEG) experiments, they established a temporal sequence for processes in a two-stage model. During the first stage, which takes place at around 300 ms after stimulus onset, an initial impression is formed. This process is associated with anterior frontomedian activity, mainly when participants consider stimuli to lack aesthetic value. A deeper aesthetic evaluation, related with broad right hemisphere activity, begins at close to 600 ms. A summary of Chatterjee (2004b) and Jacobsen and Höfel's (2003) models of aesthetic appreciation is given in Table 1.

In order to explore the relation between Chatterjee (2004b) and Jacobsen and Höfel's (2003) models and the 2004–2006 neuroimaging results, we will address issues related with the temporal span of the cognitive processes, decision and attention, and emotional engagement, separately.

However, before we do so, we feel it is important to underscore the fact that our main objective is to provide an integrative picture which can serve as the source for novel hypothesis. One of the main challenges faced by the field of neuroaesthetics, as rightfully pointed out by Chatterjee (2011), is the reliance on the reverse inference, that is, considering activity in specific brain regions to be an indication of the involvement of given cognitive processes. The impressive growth of our knowledge of the neural underpinnings of aesthetic appreciation owes a great deal to neuroimaging studies. In many cases, however, researchers have inferred that participants were performing certain cognitive or affective operations from the resulting brain activity. If such brain regions were known to be related with single specific cognitive processes this would not be a problem. With very rare exceptions, though, this has not been the case – the same brain region may be involved in several diverse processes. But Poldrack (2006) does note that the reverse inference can constitute the source for novel hypotheses that can be tested in subsequent studies. Hence, when integrating neuroimaging results with Chatterjee (2004b) and Jacobsen and Höfel's (2003) models in the following sections, we do so aiming to stimulate the formulation of hypotheses to be tested in future studies, in line with Chatterjee's (2011) caveat.

2.3.1. Temporal span

Only the study by Cela-Conde et al. (2004) was well suited, due to the temporal resolution of MEG, to test the sequence of activities suggested by Chatterjee (2004b) and, especially, Jacobsen and Höfel (2003). It reported left prefrontal dorsolateral cortex activity in the range of 400–900 ms after stimulus onset. Thus, MEG studies partially support the temporal sequence proposed by Chatterjee (2004b) and Jacobsen and Höfel (2003), but it is not fully consistent with the localization of brain activity specified in Jacobsen and Höfel's (2003) model. Specifically, whereas Jacobsen and Höfel's (2003) early activity was identified in the frontomedian cortex, especially while participants viewed stimuli they rated as lacking aesthetic appeal, Cela-Conde et al.'s (2004) early activity was circumscribed to the dorsolateral prefrontal cortex, especially while participants viewed stimuli they rated as beautiful.

We believe that this discrepancy can be accounted for by the differences in the stimuli used in both studies and the kind of statistical contrasts they explored. Whereas Cela-Conde et al. (2004) presented their participants with a broad array of artistic and non-artistic abstract and representational visual stimuli, Jacobsen and Höfel (2003) used a relatively homogeneous pool of abstract geometric patterns that varied in complexity and symmetry. In addition, Jacobsen and Höfel's (2003) results emerge from contrasting beauty judgments with symmetry judgments, and Cela-Conde et al.'s (2004) reported activity refers to the difference between ratings of "beautiful" and "not-beautiful". Hence, while there was more activity in the dorsolateral prefrontal cortex while Cela-Conde et al.'s (2004) participants viewed stimuli they rated as beautiful than when they viewed the ones they rated as not-beautiful, there was more activity in the frontomedian cortex while Jacobsen and Höfel's (2003) participants performed beauty judgments than when they performed symmetry judgments.

Taking such methodological considerations into account allows us to understand the discrepancy between both studies. The frontomedian prefrontal cortex has been shown to be involved in self-referential evaluative judgments (Northoff and Bermpohl, 2004; Zysset et al., 2002), and it is to be expected that beauty judgments, which are subject-based, would involve self-referential processing to a greater degree than symmetry judgments, which are object-based. Jacobsen and Höfel's (2003) use of abstract geometric patterns to elicit beauty judgments might have increased the subjective elements of such judgments, where participants could only base their decision on internally generated information. In contrast, Cela-Conde et al.'s (2004) approach might have encouraged participants to base their decisions about beauty on the richer external information provided by the stimuli, such as their style, explicit content, and degree of artistry. This interpretation is in accordance with Christoff and Gabrieli's (2000) suggestion that while activity in the dorsolateral prefrontal cortex seems to be primarily involved with information generated externally, activity in the frontomedian prefrontal cortex seems to reflect the engagement of processes related with the evaluation and manipulation of internally generated information.

In sum, we suggest that Jacobsen and Höfel's (2003) results reflect the greater involvement of self-referential processing of internally generated information when rating the beauty of geometric patterns than when rating their symmetry, and that Cela-Conde et al.'s (2004) results reflect the greater involvement of processing of externally provided information related with style, content, artistic status, and so on, while viewing images rated as beautiful. Together, however, both studies show that aesthetic experiences involve an early phase of evaluation, which can be mainly driven by internally or externally elaborated information. It seems implausible that such evaluation actually represents the final decision arrived at by the participants. More likely, this early brain activity associated with evaluative processes represents a fast impression formation which influences other processes related with attention, perception, response selection, and so on, but which may be crucial for decisions to continue or interrupt engagement with the stimulus.

2.3.2. Decision and attention

Decisions about the beauty of stimuli seem to be mediated by the dorsolateral prefrontal cortex (Cela-Conde et al., 2004), supporting Chatterjee's (2004b) model. The prediction by Jacobsen

Table 1
Chatterjee's (2004b) and Jacobsen and Höfel's (2003) models of aesthetic appreciation. Comparison of the time course of brain activity underlying aesthetic appreciation predicted by both models.

Temporal span	Cognitive process	Main regions involved	
		Chatterjee (2004b)	Jacobsen and Höfel (2003)
Early latencies	Visual processing	Occipital	
Intermediate latencies 300–400 ms	Initial impression		Anterior frontomedian
Undetermined latencies	Attention given to stimuli shape and color features	Frontal–parietal	
Undetermined latencies	Attributional experience of stimuli	Temporal	
Late latencies <600 ms	Aesthetic evaluation	Frontal–parietal	Right hemisphere
Late latencies	Enhancement of aesthetic experience	Frontal–parietal–temporal	
Undetermined latencies	Emotional engagement	Medial temporal	
	Deep aesthetic experience	Medial and orbitofrontal	
		Subcortical	

and Höfel's (2003) model related with negative aesthetic evaluation is supported by the frontomedian prefrontal cortex activity identified by Jacobsen et al. (2006), who, importantly, used the same kind of stimuli as Jacobsen and Höfel (2003).

Regarding attention given to the stimuli as a function of their symmetry, Jacobsen et al. (2006) reported that judgments of beauty activated mainly the frontomedian cortex, but also the left intraparietal sulcus of the symmetry network. The authors hold that aesthetic judgments of beauty rely on a network that partially overlaps with another network that underlies evaluative judgments based on social and moral cues. The attentional engagement with visual stimuli during aesthetic experiences was also found by Vartanian and Goel (2004). They reported activity in the occipital cortex when participants rated their preference for visual stimuli, reflecting an enhanced processing of certain features of preferred stimuli. These studies underscore the importance of attentional processes involved in aesthetic appreciation and their contribution to deciding about the beauty of an object or one's preference for it.

2.3.3. Affective processes

Affective and emotional processes are an integral part of our experience of artistic and aesthetic manifestations. It has been shown, for instance, that the enjoyment of music involves activity in brain regions responsible for pleasurable feelings (Blood and Zatorre, 2001; Blood et al., 1999). A fact that became evident with the initial neuroimaging studies (Cela-Conde et al., 2004; Jacobsen et al., 2006; Kawabata and Zeki, 2004; Vartanian and Goel, 2004) is that aesthetic appreciation of visual stimuli involves several different affective processes.

Despite its temporal resolution advantages, the MEG technique, used in Cela-Conde et al.'s (2004) study, is severely limited in its access to signals from the orbital and ventromedial prefrontal cortex, anterior cingulate cortex, and all subcortical brain regions. Thus, that study was unable to offer any meaningful insights into the affective side of aesthetic appreciation. However, the fMRI studies performed by Jacobsen et al. (2006), Kawabata and Zeki (2004) and Vartanian and Goel (2004) demonstrated that beauty and preference ratings correlate with activity in several brain regions related with positive affective states: temporal pole (Jacobsen et al., 2006), orbitofrontal cortex (Kawabata and Zeki, 2004), caudate nucleus, and anterior cingulate cortex (Vartanian and Goel, 2004). These results show that positive aesthetic experiences involve several different affective processes: the creation of a context based on past emotional experiences (Jacobsen et al., 2006), the assessment of the reward value of the stimuli (Kawabata and Zeki, 2004), and the integration of information from reward and cognitive processing cortical regions to elaborate an appropriate response (Vartanian and Goel, 2004).

It is worth noting that none of the 2004–2006 neuroimaging studies found significant activity in the amygdala associated with aesthetic preference ratings. On the grounds of Adolphs and Tranel's (1999) results, which suggested that the amygdala is involved in preference for visual stimuli that are generally considered to be aversive, amygdala activation might have been expected in neuroimaging studies of aesthetic appreciation, specifically when participants viewed stimuli considered as ugly.

The MEG neuroimaging technique used by Cela-Conde et al. (2004) does not allow the recording of activity in the amygdala, due to its spheroid structure. In addition, signals from medial temporal brain regions are notoriously difficult to register even with fMRI unless special measures are adopted. Thus, one possibility for the lack of significant activity associated with aesthetic appreciation in the amygdala is that Kawabata and Zeki (2004), Vartanian and Goel (2004), and Jacobsen et al.'s (2006) studies did not have adequate signal from this structure. It is true that one of Kawabata and Zeki's (2004) contrasts did reveal amygdala activity, but it entailed the comparison between their portrait and non-portrait conditions, independently of their aesthetic rating. This particular result is not surprising, given that the amygdala is a crucial element in a distributed network of face processing (Haxby et al., 2000), and its key role in analyzing and directing attention to visual social stimuli (Adolphs and Spezio, 2006).

Winston et al.'s (2007) results, which showed that activity in the amygdala followed a non-linear response pattern in relation to facial attractiveness suggest another possibility. Specifically, activity was greater for highly attractive and highly unattractive faces, compared to intermediately attractive faces. Thus, absence of amygdala activity reported in the neuroaesthetic literature may be due to the fact that neuroimaging studies have usually not included the extremely pleasant and unpleasant stimuli required to detect amygdalar activity.

3. Outstanding issues raised in recent neuroimaging approaches to aesthetic appreciation

After the 2004–2006 starting point, a number of articles continued to explore distinct aspects of the neural underpinnings of aesthetic appreciation. Hence, we will select certain aspects that we consider particularly relevant due to their important relation to the cognitive processes involved in aesthetic appreciation. These aspects are: recognition and familiarity; bottom-up vs. top-down pathways; and the influence of expertise on the neural correlates of aesthetic appreciation.

3.1. Recognition and familiarity

Together with other collative variables, Berlyne (1971) considered familiarity to exert a strong influence on the psychobiological mechanisms underlying aesthetic experiences. A number of subsequent psychological studies have shown that people usually prefer familiar stimuli, an effect currently explained under the umbrella of the processing fluency theory. Reber et al. (2004) suggested that objects vary with regards to the fluency with which they are processed. Among the features that can facilitate processing fluency they included goodness of form, symmetry, clarity, figure–ground contrast, repeated exposure and familiarity. Given that fluent processing is experienced as hedonically pleasurable, and that aesthetic experiences are strongly influenced by affective states, it follows that positive aesthetic experiences arise especially from fluent processing, such as that afforded by prototypical exemplars of a category (Winkielman et al., 2006).

Fairhall and Ishai (2008) showed that the perception of familiar content in works of art rests on several cognitive processes related with activity across a distributed cortical network. These processes include object recognition, memory recall and mental imagery. In line with the processing fluency theory, Fairhall and Ishai (2008) showed that recognition was significantly influenced by the degree of abstraction in artworks, strongly dependent on some of the features that Reber et al. (2004) and Winkielman et al. (2006) showed to determine processing fluency, such as clarity or figure–ground contrast. Specifically, participants rapidly recognized familiar objects in representational pictures, but were slower to do so for abstract or almost-abstract paintings. The study showed that recognition of familiar objects in paintings relies on brain regions related with the processing of object form, as Chatterjee's (2004b) model predicted, namely the inferior occipital gyrus (IOG) and fusiform gyrus (FG). Also, the dorsal occipital cortex (DOC), where configural relationships are processed, and the intraparietal sulcus (IPS), which is modulated by attentional demands, were activated (Fairhall and Ishai, 2008). Vartanian and Goel's (2004) results of enhanced activation in FG when representational paintings were compared with filtered paintings, were also partially confirmed.

The recognition of meaningful, familiar content in art works, as part of the representational paintings, not present in the abstract ones, is mediated by activation in the temporoparietal junction (TPJ). Kawabata and Zeki (2004) reported that the left TPJ was activated by 'beautiful' rather than 'neutral' art paintings. However, the aesthetic judgments of representational and indeterminate paintings resulted in virtually identical ratings of affect (Ishai et al., 2007). Therefore, the stronger activation of TPJ, evoked by representational paintings, cannot be explained by the affective component of aesthetic preference. Crucially, Kawabata and Zeki's (2004) experimental protocol included a stimuli pre-selection procedure, which required participants to preview and rate all the stimuli they would be subsequently shown during the fMRI scanning session. This might have inadvertently elicited recognition processes in the task the participants performed in the scanner. Prior studies have revealed that single exposures are enough for participants to recognize previously presented art-works and to bias aesthetic ratings (Cela-Conde et al., 2002; Nadal et al., 2006). Even in the absence of explicit recognition, such pre-scanning presentation might have enhanced processing fluency of the stimuli (Reber et al., 2004; Winkielman et al., 2006).

3.2. Bottom-up vs. top-down pathways

Jacobsen et al. (2006) aimed to verify previous interpretations of the amygdala as intervening in bottom-up processing (Wright et al., 2008) by means of an aesthetic appreciation task. As we have already commented, none of the 2004 neuroimaging experiments of aesthetic appreciation found activation of the amygdala. Jacobs et al. (2006) were also unable to identify significant bottom-up amygdalar activity associated with the rated beauty of stimuli (Jacobs et al., 2006). However, they reported a top-down process related with aesthetic appreciation and argued that a top-down enhancement of amygdalar activation seems to be required when expressing aesthetic preference for low-arousal stimuli.

Cupchik et al.' (2009) study was explicitly designed to disentangle the top-down orienting of attention and bottom-up perceptual facilitation involved in aesthetic appreciation. Regarding the bottom-up pathway, Cupchik et al.' (2009) results revealed that when subjects viewed softedge paintings after receiving instructions to engage aesthetically with the stimuli there was a greater activity in the left superior parietal cortex. The authors attribute this activation to viewers' attempts to resolve the indeterminate forms in softedge paintings to construct coherent images. They believe the top-down pathway to be related with the activation of the left lateral prefrontal cortex. Specifically, the authors attribute this activation to the top-down organization of perception when participants adopted an aesthetic orientation towards the visual stimuli, which is in agreement with the general involvement of lateral prefrontal cortex in the control of cognition (Cupchik et al., 2009). This result fits with the activation during late latencies (>400 ms) of the left dorsolateral prefrontal, in Cela-Conde et al.'s (2004) study.

3.3. The influence of expertise

A number of psychological experiments have revealed significant differences in aesthetic appreciation as a function of people's experience and knowledge of art. This line of research stretches from Barron and Welsh (1952) and Munsinger and Kessen's (1964) pioneering work, to Winston and Cupchik (1992) and Hekkert and van Wieringen's (1996) more recent studies. Although such differences in aesthetic appreciation between groups with and without art experience have been described many times, few studies have set out to provide an explanation for them. The most that they have shown is that art-trained and naïve participants perceptually explore artworks differently. Eye-tracking experiments studying both kinds of participants' exploration of paintings have converged on the finding that increasing levels of expertise are related with a deeper visual exploration of the overall composition, rather then the constituent elements, which are the focus of art–naïve experts. Experts spend significantly more time looking at background features, the composition, and the color contrasts, whereas untrained viewers spend more time looking at individual figurative elements and exploring figures in the centre and foreground (Nodine et al., 1993; Vogt and Magnussen, 2007; Winston and Cupchik, 1992). These effects may be stronger for abstract than representational paintings (Zangemeister et al., 1995). Such results are coherent with purely behavioral studies such as Hekkert and van Wieringen's (1996), which revealed that features such as color and degree of realism – whose variation alters the appearance of the elements but not the overall composition– had a stronger effect on the way naïve viewers appraise paintings.

Neuroscientists are facing up to the challenge of relating these differences in aesthetic appreciation and visual processing strategies with differences between experts and nonexperts in neural activity in specific brain regions. For instance, Calvo-Merino et al. (2005) asked expert ballet and capoeira dancers, as well as non-dancers, to view short video clips of capoeira and ballet movements. Participants were instructed to rate how tiring they thought each movement was –an irrelevant task– while their brain activity was registered using fMRI. Results showed that when expert dancers viewed movements corresponding to their own style compared to the other style there was greater activity in premotor cortex, parietal areas and superior temporal sulcus, which are involved in biological motion perception. Such results were mirrored by Orgs et al.'s (2008) electroencephalographic and Cross et al.'s (2006) fMRI experiments.

Calvo-Merino et al. (2010a) subsequently attempted to further characterize the biological substrate of dance expertise. They asked 24 ballet dancers and 24 non-dancers to perform a visual discrimination task between upright and inverted dance movements. The inverted presentation of stimuli which are usually viewed upright is known to specifically disrupt processing and subsequent use of relational features in configural analysis (Busey and Vanderkolk, 2005; Diamond and Carey, 1986; Rossion and Curran, 2010). Experts were better at discriminating upright dance movements than non-experts. However, no differences were found for inverted dance movements. These results suggest that dance expertise enhances mainly configural –as opposed to featural– processing of dance movements. This result is particularly interesting, given that there seem to be two specialized routes for processing human bodies, one of which processes bodies in a configural manner, involving areas of the dorsal visual system and the premotor cortex, and another, which appears to be specialized in the processing of specific details of body posture, and is part of the ventral visual processing stream, encompassing the extra-striate body area (Urgesi et al., 2007).

Calvo-Merino et al.'s (2010b) study was designed to determine the relative contribution of these two body-processing streams to aesthetic appreciation. In this study, transcranial magnetic stimulation was applied over the dorsal and ventral pathways while participants indicated the extent to which they liked several dance postures. Results showed that the procedure especially interfered with aesthetic appreciation when the stimulation was produced over the dorsal pathway, that is, the one underlying configural processing (Urgesi et al., 2007). These results reveal that general configural aspects of dance play a greater role in aesthetic appreciation than specific features of body postures. Although this particular study did not include expert dancers, it follows from this line of researchers that expertise in dance enhances the neural mechanisms underlying configural body processing, the same ones that seem to be crucial for aesthetic appreciation of dance.

Kirk et al. (2009a) designed a study to characterize the biological underpinnings of architecture expertise. The authors wished to determine whether architecture experts and nonexperts showed any differences in brain activity related with processes of perception, memory or reward while viewing buildings. Architects and non-architects were asked to indicate, on a 5-point scale, how appealing they found a series of photographs of buildings, stimuli for which only the group of architects were experts, and faces, stimuli for which both groups evidently had equal expertise.

The results showed that, independently of appeal, there were differences in activity between architects and non-architects in the hippocampus and precuneus while viewing the buildings. In addition, there was significant activity related with appeal ratings in three distinct brain regions. First, activity in the medial orbitofrontal cortex correlated positively with the level of appeal for the groups of expert and nonexperts while viewing both kinds of stimuli, faces and buildings. However, the increase in activity in this brain region was stronger for the architects viewing images of buildings. Second, anterior cingulate activity was also significantly associated with appeal ratings, and it was similar for both groups of participants while viewing faces. This was not so, however, when participants viewed images of buildings. Here activity increased with appeal for experts and decreased for nonexperts. Third, activity in the nucleus accumbens correlated positively with appeal for both groups of participants and both stimuli kinds (Kirk et al., 2009a).

Overall, Calvo-Merino et al. (2010b) and Kirk et al.'s (2009a) study reveal how expertise in visual aesthetic activities, such as dance and architecture, can lead to differences in perceptual, representational and affective processes involved in aesthetic experience. Experts seem to rely more than nonexperts on configural processing and their stored knowledge of facts pertaining to their particular domain of expertise while viewing visual stimuli depicting objects from such domain. They also attribute greater reward value and engage self-monitoring strategies to a greater extent that nonexperts. These differences seem to be in contrast with the common activity observed in brain structures involved in core pleasure sensations, such as the nucleus accumbens. If anything, these studies have clearly shown that expertise has a complex and multifaceted impact on the neural correlates of aesthetic appreciation, and that this line of research constitutes fertile ground for future inquiry.

4. Summary and future prospects for neuroaesthetics

Each of the studies mentioned above focuses on particular aspects of the neural correlates of aesthetic appreciation. However, as we noted at the beginning, there is no straightforward link from a particular kind of neural network activation to the subjective experience of considering a given stimulus to be "beautiful" – leaving aside, moreover, that there is no clear definition of "beauty". Instead of a linear scheme of stimulus–activation–appreciation, akin to a bottom-up perceptive "module" postulated by Fodor's (1983) architecture of mind, we would like to propose a different view, initially grounded on Chatterjee's (2004b) model.

Table 2 shows how Chatterjee's (2004b) model can be related to neuroimaging results on aesthetic appreciation.

The interactions among cognitive and affective processes predicted by the model have not been adequately tested yet, due to the lack of sufficient temporal resolution of the fMRI technique. The notion of connectivity has largely been considered by anatomists, neurologists and psychologists to be at the core of explanations of consciousness (Crick and Koch, 1990). Since the times of von der Malsburg (von der Malsburg and Schneider, 1986) consciousness has been associated with the presumed synchronization of neuronal network activity in the establishment of neuronal ensembles (Young and Eggermont, 2009). Thus, any connectivity identified between brain regions known to be relevant for specific mental processes, or their altered functioning, is of great interest for the delineation of the mind's architecture.

Determination of the correlation between fMRI time series is grounded on the promise of discovering "functional connectivity" between brain sites. This is a common procedure, with its pros and cons. However, a general, methodological question can be posed, namely, whether the temporal resolution of fMRI records is adequate to gauge neural synchronization. Given that fMRI averages neural activity in the order of seconds, this time interval seems too long to deduce the presence of functional connections responsible for the initial evaluation of visual stimulation. It seems that other neuroimaging techniques, such as MEG or EEG, which have a much higher temporal resolution, might be combined with fMRI in the experimental studies in order to obtain a higher accuracy regarding the temporal span of neural activation.

However, in addition to these and other methodological issues (Nadal and Pearce, in press), the emerging field of neuroaesthetics also faces challenges of a conceptual nature. Probably the most controversial unresolved matter is whether the neurosciences should be limited to exploring the biological foundations of aesthetic experience, or whether this approach can also make a meaningful contribution to our understanding of artistic activities. Four arguments have been put forward to support the contention that neuroaesthetics cannot account for artistic behavior: (i) its strict focus on beauty, preference, liking, and so on; (ii) its search for general principles and neglect of particular aspects; (iii) its disregard for contextual features; (iv) its attempts to reduce art production and appreciation to general neurobiological mechanisms.

Regarding the first of these four arguments, Brown and Dissanayake (2009) have explicitly stated that neuroaesthetics

Table 2
The relation between Chatterjee's (2004b) model and the neuroimaging results on aesthetic appreciation. It shows how Chatterjee's (2004b) neurocognitive model of aesthetic appreciation provides an integrative framework to interpret the overall pattern of results obtained by neuroimaging results.

Attentional processes	Fronto-parietal networks	Fairhall and Ishai (2008)
Attributional networks	Ventral visual stream	Fairhall and Ishai (2008)
		Vartanian and Goel (2004)
Experience of the aesthetic quality	Feed-back/feed-forward links	Cela-Conde et al. (2004)
		Jacobsen et al. (2006)
		Cupchik et al. (2009)
Emotional reward enhancement of aesthetic experience	Anterior medial temporal lobe	Kawabata and Zeki (2004)
	Medial and orbitofrontal cortices	Cela-Conde et al. (2004)
	Subcortical structures	Vartanian and Goel (2004)
		Jacobsen et al. (2006)
		Jacobsen et al. (2006)
		Kirk et al. (2009a,b)
		Kirk et al. (2009a,b)

cannot in principle deal with the arts, on account of its emphasis on aesthetic phenomena: "Aesthetic emotions are unquestionably an integral part of the arts, but they are neither necessary nor sufficient to characterize them. Thus, a narrow focus on aesthetic responses is ultimately a distraction from the larger picture of what the arts are about" (Brown and Dissanayake, 2009, p. 54). Indeed, many artistic manifestations around the world and throughout history have been completely unrelated to beauty. Besides portraying beauty, art has been –and continues to be– created to intimidate, to express sorrow, to extol a society's grandeur, to make us reflect on humanity's and our own existence, among many other functions. In fact, contemporary western art has seen many instances of works that are conceived as a reaction against beauty as an artistic concept. As noted by Danto (1997), "the connection between art and aesthetics is a matter of historical contingency, and not part of the essence of art" (Danto, 1997, p. 25). Moreover, artworks rarely serve a single purpose. They have different meanings for different people, in different context, and at different times. Brown and Dissanayake (2009) firmly believe that neuroaesthetics cannot grasp the emotional, formal, cultural, and intentional plurality inherent to the production and perception of art.

The second issue refers to the different emphasis placed by the traditional approach to the arts and neuroaesthetics on the general and the particular. Neuroaesthetics, in its approach to art, seeks general relations between cognitive processes and neural mechanisms when encountering an artwork, not necessarily any particular one though. Conversely, humanist researchers are interested in addressing specific issues related with a particular work of art. According to Massey (2009), "Neurology is, then, of great value in exploring the 'how' of aesthetic processes, if not necessarily the 'why' or the 'what for,' or in helping to decide whether one work of art is of greater value than another" (Massey, 2009, p. 18). In this sense, whatever the neurosciences can reveal is completely irrelevant for a meaningful understanding of art. Tallis (2008a) goes even further in dismissing the possible contribution of neuroaesthetics to the arts as an extreme expression of the belief that the contents of human consciousness can be explained (away) in terms of neural activity: "[Neuroaesthetics] casts no light on the specific nature of the objects and experiences of art or the distinctive contribution of individual artists. Nor does it offer any basis for the evaluation of art as great, good, or bad. In short, neuroaesthetics bypasses everything that art criticism is about" (Tallis, 2008a, p. 19).

The third argument charges neuroaesthetics with taking stimuli and participants out of their natural contexts. In Tallis' (2008a) words: "Paintings are treated as mere isolated stimuli or sets of stimuli. [...] The works and our experiences of them are divorced from their cultural context, and from the viewer's individual history" (Tallis, 2008a, p. 20). Neuroimaging methods have required that experiments include long successions of stimuli, most often without any kind of contextual information, to large numbers of naïve participants. Moreover, experimental settings do not foster natural engagement with the artworks.

The fourth point noted above argues that human aesthetic experience cannot be meaningfully understood in terms of neurobiological mechanisms that underlie other activities unrelated with art, some of which are even shared with other nonhuman animals. Such reduction fails to account for the distinguishing features of the human experience of great works of art with regards to everyday perceptual experiences: "Tickling up the mirror neurones does not explain why Donne's stanzas should have the particularly intense effect they (sometimes) do" (Tallis, 2008b).

The big question, thus, is what are the prospects –in the face of such arguments –for neuroaesthetics? Can it ever make meaningful contributions to understanding the human propensity to produce and appreciate art? We believe that there is no certain *a priori* response to this question. There is no reason why studies cannot in principle address some of the aforementioned issues. In fact, we believe that such criticisms may constitute the source for interesting avenues to be explored in future studies. Researchers could, for instance, decide to study the neural correlates of aesthetic appreciation under different contextual conditions, whether different kinds contextual information influences the neural processes underlying aesthetic appreciation for different kinds of artworks in different ways, and so on. It is up to neuroscientists to come up with ingenious designs for studies that can begin overcoming some of the limitations pointed out above and, as a consequence, producing findings which are relevant to other approaches to aesthetic appreciation, such as art theory or philosophy.

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