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INTERPLAY OF THE TWO CULTURES: NEUROAESTHETICS

Neuroaesthetics: themes from the past, current issues, and challenges for the future

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Abstract Neuroaesthetics is a growing field of research concerned with the biological foundations of aesthetic experiences and artistic activities. In this paper we trace the major milestones in the history of neuroaesthetics, from British Empiricism to current neuroimaging studies, emphasizing the continuity of certain basic assumptions and controversies. Thereafter we turn to an issue that has received attention only recently: differences between men and women in the neural underpinnings of aesthetic preference. We argue that the combination of neuroimaging techniques and evolutionary reasoning affords the possibility of an integral understanding of the biological foundations of aesthetic experiences. Finally, we summarize some challenges neuroaesthetics will have to face in the future.

Keywords Neuroaesthetics · Aesthetic appreciation · Beauty · Sex-related differences

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1 Introduction

It can be safely argued that the field of neuroaesthetics has been growing steadily for the past decade (Chatterjee 2011; Nadal and Pearce 2011). Never before have there been so many researchers devoting their resources to characterizing the biological foundations of aesthetic experience and artistic activities. Although much of this research today involves the use of novel neuroimaging techniques, the interest in this topic is by no means new. Here we will trace the first attempts to understand the neural processes that support aesthetic experience back to the British Empiricists of the eighteenth century. Our historical survey will reveal the continuity of certain themes, such as the relation between pleasure and beauty, and the persistence of certain controversies, such as the subjective or objective origin of the aesthetic experience.

Despite the permanence of some issues and research topics, the use of neuroimaging techniques has afforded researchers the chance to ask a whole new set of questions regarding the biological processes involved in aesthetic experience. In a later section of this paper we present the work of our research group aimed at characterizing the differences between men and women in the neural processes underlying beauty appreciation, which would have been impossible to achieve without the development of neuroimaging. We also present our work as a case for the integration of the neural and evolutionary perspectives, which we believe will, ultimately, lead to a comprehensive understanding of what makes our species so prone to engage with the world with an aesthetic orientation. We will end by pointing out some of what we believe are the main challenges that neuroaesthetics will have to face in the future.

2 The quest for the neurobiological underpinnings of aesthetic appreciation

Current research aimed at characterizing the neural mechanisms underlying the aesthetic experience owes much to the pioneering work of Changeux (1994), Ramachandran and Hirstein (1999), and Zeki (1999). It was Zeki (1999), in fact, who introduced the term *Neuroaesthetics* when referring to a potential field dealing with the biological underpinnings of the aesthetic experience. Since the 1990s, this field has significantly grown, matured, and diversified (Chatterjee 2011; Nadal and Pearce 2011). One of the main difficulties faced by neuroaesthetics is, however, the little agreement among researchers on its proper object of study. Even the appropriate way to characterize the aesthetic experience has been a topic of heated discussion with neuroaesthetics, as it has been within philosophy for centuries. In this paper we will refer to the aesthetic experience in the broadest possible terms to refer to any act of perception that is experienced on a continuum from the pleasant to the unpleasant. This includes the experiences of enjoying looking at, listening to, smelling, touching or tasting artificial or natural objects or phenomena, as well as the negative counterpart of disliking the experience of perceiving them. By no means is this intended as a consensus characterization—if there even is one—and we refer the reader to specialized treatises for a more thorough discussion on the appropriate definition of aesthetic experience (see for instance Shusterman and Tomlin 2008).

Although, in a strict sense, the history of neuroaesthetics would not span more than 15 years, the quest to understand the neural processes that make the aesthetic experience possible can be traced back almost to the beginning of philosophical aesthetics. This intent is especially clear in the works of British empiricists (Moore 2002; Skov and Vartanian 2009). Although Hobbes, Berkeley, Locke and Hume are the most notable representatives of this school, it was Burke (1757) who provided the most explicit argument about the physiological basis of aesthetic experience. Given that this is the main topic of this paper, we will concentrate on Burke's early psychobiology of aesthetics and avoid leading the reader into a purely philosophical excursus. Within the frame of the Cartesian understanding of the human body as a machine and animal spirits acting through the nerves to produce movements and convey sensory information, Burke (1757) argued that aesthetic experiences were grounded on the same physical mechanisms as pleasant and unpleasant emotions. Thus, he believed that people find objects, landscapes, and other people beautiful because such stimuli relax our nervous system, just as emotions such as love and tenderness do. On the other hand, stimuli and events are experienced as sublime when they produce the characteristic effects of pain, fear, and terror on the nervous system.

Some of Burke's contemporaries continued to develop this physiological approach to aesthetic experience. Webb (1769), for instance, argued that both music and emotion excited vibrations in the nerves and produced diverse movements of the animal spirits, ranging from the violent agitation that caused anger or indignation, to the soft and calm vibrations that characterize love and wellbeing. Price (1810) believed that there was an intimate relation between feelings of curiosity and picturesque aesthetic experiences and that such feelings were related to the return of nervous fibers to their normal tone. The quality of the picturesque, he wrote, "corrects the languor of beauty, or the tension of sublimity" (Price 1810, p. 89).

The widespread and lasting influence of Kant's (1790/1892) transcendental perspective, as noted by Moore (2002), separated the aesthetic experience from emotion and sensory pleasure, and halted this first physiological approach to aesthetic experience. In fact, it fell out of the mainstream until nineteenth century pioneering neuroscientific studies began clarifying the relation between mental phenomena and the brain's anatomy and function. A renewed interest in the relation between pain and pleasure and aesthetics appeared in the midst of this emerging neuroscience. Marshall (1892, 1893) updated the Empiricists' relation between beauty and pleasure, arguing that "The beautiful is that which produces effects in us that are (relatively) permanently pleasurable in revival. The ugly, on the contrary, is that which produces effects of (relatively) permanent painfulness in revival" (Marshall 1893, p. 15). Allen (1877) went further and ventured a physiological account of the pain and pleasure foundations of different aesthetic experiences. He defined pain as the subjective experience of damage or insufficient nutrition of any bodily tissue and pleasure as the subjective experience of the normal amount of functioning of such tissue. He noted, however, that such normal function is not usually felt as pleasurable, but as a neutral state. There is only a difference of degree between the pain and pleasure related with survival-related activities and the pleasure and pain underlying aesthetic experiences. The pleasure and pain associated with sight and sound, he noted, are subtle, and their perception requires attention. In most cases, therefore, the objects that evoke these sensations are merely intellectually discriminated as beautiful or ugly, while not seeming pleasurable or painful. In sum,

> The aesthetically beautiful is that which affords the Maximum of stimulation with the Minimum of Fatigue or Waste, in processes not directly connected with vital functions. The aesthetically ugly is that which conspicuously fails to do so; which gives little

> stimulation, or makes excessive and wasteful demands upon certain portions of the organs. But as in either case the emotional element is weak, it is mainly cognised only as an intellectual discrimination (Allen 1877, p. 37).

As neuroscientists' knowledge of brain structure and function advanced, neurologists were able to examine the relation between brain injuries and artistic and aesthetic production and appreciation. The relation between aphasia, on the one hand, and musical and pictorial activities, on the other, received special attention due to the apparent uniqueness of both human language and art. Dupré and Nathan (1911), Souques and Baruk (1930), Alajouanine (1948), Luria et al. (1965), Gourevitch (1967) and Zaimov et al. (1969) described several cases of aphasic artists. Despite their great inherent interest, this kind of "informative anecdotes" (Chatterjee 2011, p. 54), accumulated throughout the twentieth century—together with a number of accounts on the impact of diverse forms of dementia on artistic and aesthetic activities—have often been described in imprecise terms, and their implications have been difficult to assess due to the absence of an adequate theoretical framework. Meaningful conclusions regarding the impact on artistic and aesthetic activities of different neurological conditions, such as achromatopsia, unilateral spatial neglect, visual agnosia, aphasia, epilepsy, Alzheimer's disease or frontotemporal dementia, only emerged after Bäzner and Hennerici (2006), Bogousslavsky (2005; Bogousslavsky and Boller 2005), Chatterjee (2004b, 2006), Miller and Hou (2004) and Zaidel (2005, 2010) reviewed and analyzed such cases together.

These integrative studies have, in the first place, revealed that despite artists' proficient musical or visual and motor skills, they are susceptible to the same neurological impairments that affect other people's visual, motor, auditory, and cognitive performance. In Chatterjee's (2004b) words, artists can express these deficits through their work in strikingly eloquent ways. Second, most of the artists suffering from these neurological cases continued to be artistically motivated, productive, and expressive. As noted by Zaidel (2005), personal style is usually preserved to a certain extent, owing to the extensive practice of their skill. Moreover, suffering from neurological conditions does not straightforwardly lead to an improvised quality of artworks. In several cases the effect of the condition has been aesthetically surprising and pleasing (Chatterjee 2004b). Third, certain regularities in the description of the work of artists who have suffered brain damage or neurodegenerative diseases suggest that neurological conditions can have diverse and distinctive effects on art. For instance, whereas spatial disorganization, distortion and neglect in painting are more common in stroke patients, artists with Alzheimer's disease gradually lose the ability to represent the world with precision, despite being able to use colour and form in aesthetically appealing ways. Finally, these studies have also demonstrated that there is no single brain region or hemisphere which can be thought to be the centre for art, aesthetics or creativity (see Cela-Conde et al. 2011 for a summary). Given the nature of the issue being studied, however, these results are based on mere observation and description, not proper empirical data. Nevertheless, significant headway in this sense is being made after Chatterjee et al. (2010) created an objective system allowing the experimental testing of the effects of brain lesion on artistic creation and appreciation (Bromberger et al. 2011; Chatterjee et al. 2011).

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 under controlled conditions, and to correlate appreciation and enjoyment of music, painting, architecture, sculpture and dance, with the activity of diverse brain structures. As noted by Nadal and Pearce (2011), such studies have revealed that positive aesthetic experiences—indicated by high liking, preference, or beauty ratings—are associated with three kinds of brain activity. First, aesthetic experience seems to engage activity in cortical regions involved in top–down processing and evaluative judgment (Cela-Conde et al. 2004; Cupchik et al. 2009; Jacobsen et al. 2006; Lengger et al. 2007). Second, many studies report activation of cortical and subcortical components of the reward circuit related with different aspects of affective processing. Namely, the orbitofrontal cortex, which seems to be involved in the representation of reward value, has been associated with positive aesthetic experiences of music (Blood and Zatorre 2001; Blood et al. 1999), architecture (Kirk et al. 2009a), and paintings (Cupchik et al. 2009; Kawabata and Zeki 2004; Kirk et al. 2009b). Activity in the anterior cingulate cortex, possibly related to the monitoring of one's own affective state, has also been identified while rating paintings (Cupchik et al. 2009; Vartanian and Goel 2004), architecture (Kirk et al. 2009a) and music (Blood et al. 1999). Subcortical components of the reward circuit, including the ventral striatum, the caudate nucleus, the substantia nigra, and the amygdala, have been shown to be involved in the aesthetic experience by a considerable number of studies (Bar and Neta 2007; Blood and Zatorre 2001; Blood et al. 1999; Brown et al. 2004; Cupchik et al. 2009; Gosselin et al. 2007; Mitterschiffthaler et al. 2007; Kirk et al. 2009a; Koelsch et al. 2006; Salimpoor et al. 2011; Vartanian and Goel 2004). Third, an enhancement of low-and high-level visual, somatosensory and auditory cortical processing has been observed while people rated paintings or landscape photographs (Cela-Conde et al.

2009; Cupchik et al. 2009; Vartanian and Goel 2004; Yue et al. 2007), dance movements or postures (Calvo-Merino et al. 2008, 2010), and music excerpts (Brown et al. 2004; Koelsch et al. 2006), respectively.

3 New techniques, old debates: is beauty in the object or in the subject?

The use of novel methods and techniques has allowed researchers to address some of the issues raised by scholars during the past three centuries with a degree of detail previously unimaginable. Scientists are also exploring new questions, such as the role of dopamine in aesthetic appreciation (Salimpoor et al. 2011), or how context modulates activity in certain brain regions involved in aesthetic valuation (Kirk et al. 2009b). Despite the use of innovative technology and experimental designs, however, scientific approaches to aesthetics owe their main theoretical paradigms to Philosophical and Psychological Aesthetics. Scientists have, moreover, been landed with some of Aesthetics' most ancient entrenched positions and long-lasting controversies. One recurring debate refers to the objectivity or subjectivity of aesthetics: "when we call a thing 'beautiful' or 'aesthetic,' do we ascribe to it a quality it possesses by itself or one which it does not possess but which we confer upon it?" (Tatarkiewicz 1963, p. 157). Both perspectives found support among early Greek philosophers, with Pythagoreans attempting to prove the objectivity of beauty and Sophists arguing in favor of its subjectivity.

The first scientific approaches to aesthetics were clearly grounded on the notion that beauty resided in the object and, thus, that it was directly measurable. Zeising (1855), for instance, believed that the golden section was the basis of proportionality, a property inherent to everything in the universe, and that it was an essential constituent of beauty in art and nature, including the human body (Padovan 1999). Zeising (1854) grounded his argument that the golden section governs the form of flowers, crystals, and many other complex entities on careful measurements and calculations. Beauty, he believed, emerged from the presence of certain features in an object—specific proportional relations in this case. Once such features were perceived, they were valued as beautiful by the viewer. The artists' virtue lies, from this perspective, in the use and combination of such features to elicit aesthetic experiences in their audiences.

Fechner's (1876) *Vorschule der Aesthetik*, which is usually considered to mark the beginning of empirical aesthetics (Cupchik 1986), expanded this line of thinking. Fechner (1865) performed the first empirical test of the influence of the golden section on people's preference (Berlyne 1971; Green 1995). He showed his participants ten rectangles that varied in proportion from 1:1 to 2.5:1 and then asked them to indicate which one they found most pleasing, and which one they found the least pleasing. Most of the participants' responses favored the rectangles representing the golden section or similar proportions. According to Fechner (1876), 34.50 and 35.83 % of men and women chose the golden section rectangle. In fact, none of the participants selected it as the least pleasing. This, Fechner believed, constituted evidence for the argument that certain properties of the stimuli—that is to say, objective features—were generally preferred, liked, or experienced as beautiful.

The Gestalt school of psychology reacted against the atomistic conception of mental processes, especially perception, arguing that experience is nothing like a mosaic of discrete and disengaged elements, a view espoused by psychophysics. Gestalt psychologists conceived all human experience as a field where parts interact dynamically with each other, and are influenced by the nature of the whole field. Perception and understanding of objects and scenes were considered to be emergent processes, going beyond the mere recording of the elements in the stimulus. Wertheimer (1923) suggested a number of grouping principles, such as proximity, continuation, similarity or closure, which organized parts of the visual scene into wholes, such as objects, clusters, and overall scenes. Perceptual order, organization, and form are the outcome of the subject's engagement with input. The perceiver is not regarded as a passive receiver, but as an active organizing agent.

Koffka (1940) openly rejected the psychophysical approach whereby beauty is defined in terms of the physical properties of the stimulus. From the Gestalt point of view, appreciation of beauty and art emerges from the interaction of the viewer's psychological processes and the artwork's features. Koffka (1940) considered works of art to be special kinds of good gestalts, in that their constituents are placed by the demand of the whole and that the dynamic forces are particularly well balanced. An artwork is appealing as a structure, not as a collection of parts, but as a consistent entirety where each constituent requires the others. This structure is in close dynamic interaction with the viewer, who is actively organizing the artwork in one direction, and being affected by it in the other. From this perspective, thus, beauty lies in the eye of the beholder as much as in the object itself. It is, in fact, a construction produced by the dynamic interaction between subject and object. This view reconciles two opposite perspectives whose origin can be traced back to the Pythagoreans and the Sophists.

During the 1960s and 1970s, Daniel Berlyne developed a broad research program, known as Psychobiological Aesthetics, which became the starting point for contemporary experimental aesthetics. On the grounds of neurobiological findings on motivational and emotional systems, Berlyne (1971) argued that the hedonic tone induced by a stimulus depends on the level of arousal that it is capable of eliciting and the organism's current arousal level. In relation to aesthetics and art, Berlyne suggested that interest and preference for a given work, whether pictorial or musical, depend primarily on how complex such a stimulus appears to the viewer (Berlyne 1963, 1970; Berlyne et al. 1968). People were expected to prefer intermediately complex artworks over highly complex or very simple ones, given that they afford an optimal arousal level. It is here where Berlyne's (1971) interactionist perspective is clearer. By asserting that it is not the object's inherent features—complexity in this case—that influence aesthetic experience, but the way in which the spectator organizes and perceives the object, Berlyne moved away from Zeising and Fechner's strict empiricism and acknowledged the active role of the perceiver, as emphasized by the Gestalt psychologists.

The debate about the subjectivity of the aesthetic experience is alive today in neuroaesthetics, with some researchers seeking to distinguish the neural correlates of processing of objective and subjective components of aesthetics (Di Dio et al. 2007). We believe that this contradicts much of what is known about perceptual processing: "Perception is not a passive taking-in of stimuli, but an active process of synthesizing or constructing a visual figure" (Neisser 1967, p. 16). Although the starting point of perception is sensory information, its purpose is not to render the world as it is, but to provide us with an image that we can understand and is coherent with our prior knowledge about the world. In order to do so, perception is guided by inference, hypotheses, and other top–down processes, as well as context, which can strongly influence the appearance of an object. The fathers of cognitive science warned us not to fall into naïve realism; we only take a small sample of reality in, we then bend and twist it to fit the rest of our mental world, "But it is not random, this sampling of the world by the eye and the ear and the skin senses and the rest. It is a filtering, a sorting out, and finally a construction, that world we perceive directly. The nature of the filter and of the construction processes that work with it—these constitute the real philosopher's stone. It does not turn base metal into gold, but turns physical 'stimuli' into knowledge, a much more valuable transformation" (Bruner 1983, p. 66).

Psychologists have illustrated how much perception relies on assumptions and inferences by using illusions to play tricks on it. One of the many illusions considered by psychologists is the well-known Müller-Lyer illusion (see Fig. 1). Objectively, both horizontal lines are the same length. Subjectively, though, one of them seems to be longer.

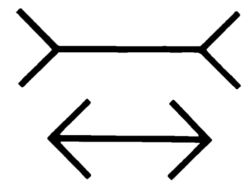

Fig. 1 The Müller-Lyer illusion

Surprisingly, these illusions, and presumably the assumptions that govern them, are influenced by practice and viewing time (Lewis 1908; Mountjoy 1958; Schiano and Jordan, 1990) as well as by age, education, culture and ecology (Berry 1968; Davis 1970; Segall et al. 1966; Pedersen and Wheeler 1983; Pinter and Anderson 1916), accentuating the importance of the subject and prior experience even in such basic perceptual processes. If people are unable to accurately perceive the objective lengths of the simple lines in the Müller-Lyer illusion, is it reasonable to expect them to perceive the objective beauty—which presumably amounts to more than line length—of complex and intricate objects, like works of art? Maybe, as in many spheres of perception, the aesthetic experience arises from the interaction of diverse object-driven and subject-driven processes. And, maybe, creating experimental conditions that aim to tease these apart will only end up removing that which is truly aesthetic from the experience: "Whether beautiful of ugly or just conveniently at hand, the world of experience is produced by the man who experiences it" (Neisser 1967, p. 3).

4 Sex-related differences in the appreciation of beauty

Despite this historical continuity in some of the main research themes, such as the relation between pleasure and beauty, and controversies, such as the objective-subjective debate, the development and increasing use of neuroimaging techniques has allowed researchers to ask many new questions about the biological underpinnings of the aesthetic experience. One of these refers to whether there are differences in the neural foundations of the aesthetic experience between men and women. Behavioral experiments have often revealed that men and women tend to award different beauty ratings to abstract and representational artworks (Frumkin 1963; Furnham and Walker 2001; Polzella 2000). Yet, it is uncertain how these sex-related differences relate to the neural correlates of decisions about aesthetic beauty.

Several studies have reported differences between men and women in brain activity related with cognitive (Bell et al. 2006; Boghi et al. 2006; Haier et al. 2005) and affective (Azim et al. 2005; Piefke et al. 2005) processes, often revealing different lateralization patterns between the sexes (Cahill 2006). Given that aesthetic appreciation relies on a number of such cognitive and affective processes (Chatterjee 2004a; Leder et al. 2004), Cela-Conde et al. (2009) hypothesized that there would be differences in brain activity while men and women rated the beauty of visual stimuli, probably related with different lateralization patterns. In order to put this hypothesis to the test they used magnetoencephalography (MEG) to record brain activity while participants viewed images of unfamiliar artworks from different genres, and "natural" photographs depicting diverse objects and landscapes, urban and rural. Participants were asked to indicate whether they found each image beautiful or not. They also turned to comparative neuroanatomy to attempt to determine whether any possible differences between the sexes could be due to evolutionary processes that occurred along the evolution of the human lineage or in an earlier primate ancestor.

Cela-Conde et al.'s (2009) results showed that during the initial 300 ms (milliseconds) after stimulus onset there were no differences in brain activity owing to beauty rating or sex. During the 300- to 700-ms interval, however, activity was greater in parietal regions for stimuli rated as beautiful than for those rated as not beautiful. Moreover, whereas in women this activity was found in both hemispheres, in men it was mainly restricted to the right hemisphere (see Fig. 2). Cela-Conde and colleagues' (2009) analysis also revealed small foci of activity in areas of the left hemisphere, believed to be involved in somatosensory (BA 3, 43) and in motor (BA 4, 6) processes.

Cela-Conde et al. (2009) paid special attention to activity in the angular gyrus, which was greater for stimuli

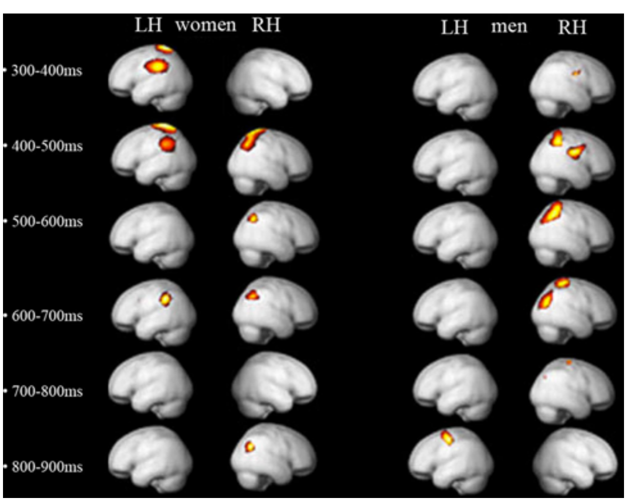

Fig. 2 Cela-Conde et al's (2009) results. The column of time intervals *on the left* shows the sequence of activation for each 100 ms window from 300 to 900 ms. The two columns of brain illustrations *on the left* show activations in women's left and right hemispheres at each time window. The two columns of brain illustrations *on the right* show the same for men

rated as beautiful in both sexes, and was sustained for a relatively long interval of time (500–600 ms for both men and women, and again 700–800 ms for men and 800–900 ms for women). Angular gyrus activity had previously been associated with the processing of categorical and coordinate spatial relations (Baciu et al. 1999; Jager and Postma 2003). The involvement of angular gyrus activity during non-canonical as opposed to canonical viewing of objects (Kosslyn et al. 1994; Terhune et al. 2005) may help interpret the differences in this region's activity in relation to beautiful and not-beautiful stimuli. Unusual orientations can be described as non-canonical—a cone standing on its point and not on its base, for instance. It would seem that unusual presentation of objects, by inverting their common orientation or by altering their natural color, influences key aspects of the appreciation of beauty, a view that has been espoused by a number of investigators (Berlyne 1970, 1971; Humphrey 1973). Similarly, fauvism, which depicts unusually colored objects, has been associated with distinctive neural correlates of visual perception (Zeki and Marini 1998). Accordingly, Cela-Conde and colleagues' (2009) results suggest that unexpected or ambiguous depictions of familiar objects, which require spatial abilities of rotation and transformation, are a primary component of aesthetic preference for both sexes, as predicted by Zeki's framework (2001, 2004).

Cela-Conde and colleagues' (2009) results clearly show that activity in the parietal regions is bilateral in the case of women but lateralized to the right hemisphere in the case of men. Many studies have found that visual processes tend to be hemispherically asymmetrical in men and more symmetrical in women (Amunts et al. 2007). The lateralization differences between men and women identified by Cela-Conde et al. (2009) can be explained by Kosslyn's (1987) notion of two separate processes that code and represent two different kinds of spatial relations among objects. Categorical spatial relations refer to positions of objects or their parts in broad categories of location regarding other elements, such as "above or below," "left or right," "in front or behind," "inside or outside." These categorical spatial relations play a role in tasks that do not require a precise location. Conversely, coordinate spatial relations involve more precise metrical information about distances among objects. Hugdahl et al. (2006), for instance, have noted that men tend to use coordinate spatial relations in mental rotation tasks, whereas women tend to process spatial relations in a categorical fashion. These strategies are associated with activity in different hemispheres. The left hemisphere seems to be more involved in the exploration of categorical spatial relations, whereas processes in the right hemisphere seem to be essential for the computation of coordinate spatial relations (Baciu et al.

1999; Chabris and Kosslyn 1998; Okubo and Michimata 2004). Hence, it appears that women and men engage different strategies of spatial analysis during aesthetic preference activity. Strongly lateralized activity in the right hemisphere suggests that men use coordinate-based strategies. Conversely, activity in both hemispheres, although mainly and longer in the left hemisphere, suggests women rely on categorical strategies more than men do.

5 Phylogenetic implications

It is generally accepted that the appearance of the capacity to use of symbols, to appreciate the beauty of objects and to create them marked a significant turning point in the evolution of *Homo sapiens*. Although the ability to make beautiful objects has been taken as an indication of a capacity to appreciate beauty (Ambrose 2001), it is unclear when this capacity first appeared in the human lineage (Cela-Conde and Ayala 2007). The evolutionary changes associated with the necessary cognitive development for appreciating the beauty of objects is often linked to the appearance of symbolism (Gabora 2005). However, there is no universal agreement as to what counts as evidence for symbolism and symbolic behavior. Alternative proposals include the manufacture of any symmetric object without any apparent practical use (Bednarik 1995, 2003; Marshack 1996), or of explicitly decorative ornaments, or of the pigments used to paint them (Bar-Yosef Mayer et al. 2009; Bouzouggar et al. 2007; d'Errico et al. 2005; Texier et al. 2010). For some authors, the construction of objects resembling a human body would be sufficient evidence of symbolism (Marshack 1996), whereas others assert that only realistic paintings or sculptures, i.e., works of art, can be considered as true manifestations of a symbolic capacity (Appenzeller 1998).

In any case, the production of decorative and artistic objects is widely considered as a fundamental stage in the emergence of modern human behavior. The appearance of the capacities to appreciate beauty and to produce beautiful objects has been related with certain forms of social behavior, language, a variety of mental capacities and neurological functions, and even diseases, such as schizophrenia. Together with social organization, the cognitive capacity expressed by the use of symbolism may have decisively contributed to the demographic expansion and geographic dispersion of *Homo sapiens* (Mellars 2006). One of the most popular explanations for the perception of beautiful features in objects, and for the tendency to decorate the human body, is sexual selection (Miller 2000, 2001).

Cela-Conde et al. (2009) believed that their results could throw some light on the evolution of the neural underpinnings of aesthetic appreciation. A way to trace the evolutionary roots of the gender-related differences related with aesthetic preference is to determine whether the differences involve brain regions exhibiting primitive or derived traits. They reasoned that if the gender-related differences they identified were located in relatively conserved brain regions they were probably inherited from our primate ancestors. If, conversely, differences between men and women appeared in brain regions known to have undergone considerable modifications after the human and chimpanzee lineages split, it is likely that they were due to evolutionary processes that were especially relevant to the hominin way of life.

When compared with monkeys and apes, the human parietal cortex exhibits a number of derived aspects. Humans differ from other primates in certain features related with the cortical representation of the magnocellular visual pathway. Processing along this path is responsible for the analysis of motion, perspective, relative size of objects, and depth (Preuss and Coleman 2002). The human brain area V3A (a secondary visual area) is sensitive to motion cues and uses them to extract 3-D information, whereas the monkey area V3A does not share this function (Orban et al. 2004). By means of comparative fMRI data and computerized brain warping, Orban and colleagues (2004) have suggested that the ventral and dorsal visual streams have not evolved equally along the human lineage. Rather, the brain regions that constitute the ventral stream, related with object representation and categorization, have undergone a smaller expansion than those of the dorsal stream, which are involved in the representation of space and the analysis of visual information to organize action. The parietal areas of the dorsal stream receive only information from the magnocellular system, which support the aforementioned idea of an enhancement of the magnocellular cortical representations during human evolution (Barton 2006).

It appears thus, that differences in activation in parietal brain regions observed during Cela-Conde and colleagues' (2009) aesthetic preference task owe to evolutionary processes that took place after the separation of the chimpanzee and human lineages, and that they probably had significant effects on spatial cognition. The next question is whether it is possible to identify the cladistic event within the hominin lineage that accounts for this evolutionary modification. According to Bruner et al. (2003), parietal cortex development was such a crucial event in the evolution of the brain of modern humans that it "may have represented a key to surpass the encephalization constraints imposed by the archaic structural model." The differences between the decorative objects found in Neandertal and modern human sites support that idea of a "modern brain" capable of appreciating beauty and exploiting this capacity in different ways (Appenzeller 1998). Cela-Conde and colleagues' (2009) results suggest that parietal regions of the brain of modern humans, which exhibit clearly derived traits, have a crucial role in the visual appreciation of beauty.

In sum, given that the dorsal visual pathway has been subjected to evolutionary pressures that have led to the aforementioned modifications during human evolution, it can be assumed that sex-related differences in this pathway appeared after the human and chimpanzee lineages split. It can also be hypothesized that the sex-related differences in brain processes involved in aesthetic preference identified by Cela-Conde et al. (2009) are related to events of significant importance throughout human evolution.

Silverman and Eals' (1992) "hunter-gatherer hypothesis" of gender differences in spatial abilities provides a plausible interpretation for these differences. They argued that the differences in spatial ability between men and women were associated with the division of labor between the sexes in hunting and gathering. Tracking animals and foraging for plant food involve different spatial scenarios and, hence, require different kinds of spatial skills. Silverman and Eals (1992) suggested that abilities involved in hunting include the orientation in relation to objects and locations that may be in or out of view, and thus require cognitive transformations that allow keeping an accurate orientation while moving. Conversely, foraging requires recognizing and remembering the contents of varied object assemblies and the spatial relations between objects.

The hunter-gatherer hypothesis does not regard gender differences in the performance of spatial tasks as the product of different levels of a single ability, but as the result of the use of different spatial strategies that involve different abilities. Women tend to be more aware than men of objects around them, including those that seem irrelevant to the current task (Silverman and Eals 1992), whereas men out-perform women in navigation tasks (Silverman et al. 2000). Men tend to solve navigation tasks by using orientation-based strategies involving distance concepts and cardinal directions, whereas women tend to base their activities on remembering the location of landmarks and relative directions, such as "left from," or "to the right of" (Silverman et al. 2000). An experimental study involving seven extant ethnic groups, has provided support to the hunter-gatherer hypothesis of human spatial gender differences (Silverman et al. 2007). In all seven hunter-gatherer groups, men scored significantly higher than women did in a test of 3-D mental rotations.

Thus, Cela-Conde and colleagues' (2009) study suggests that sex-related differences in the neural correlates of aesthetic appreciation seem to be related with the engagement of different spatial cognition strategies, which might have originated as a result of the division of labor between the sexes in hunting and gathering during the Pleistocene.

6 Conclusions and future challenges for neuroaesthetics

For almost 150 years, since Fechner's (1876) seminal work, have psychologists applied scientific methods to understand the cognitive processes that underlie the aesthetic experience. From the beginning of the 21st century they were joined by researchers interested in the neurobiological mechanisms that endow our species with such unparalleled capacity, leading to the new field of neuroaesthetics. In this contribution we have attempted to show that the intellectual roots of neuroaesthetics sink deep into the thinking of British empiricists, especially Burke's notion of a relation between the experience of beauty and the biological mechanisms of pleasant emotions, and between the experience of ugliness and the biological mechanisms of unpleasant emotions. We have also attempted to show how neuroaesthetics has inherited many of its questions, motivations, and debates from traditional philosophical aesthetics, such as the debate between subjective and objective approaches to beauty. Finally, we have also shown how new research tools, such as neuroimaging, afford a wealth of possibilities for researchers interested in the biological features make our species uniquely aesthetic.

We feel that one of the main challenges faced by neuroaesthetics refers to the way its main object of study—aesthetic experience—is conceived. It is too easy to loose sight of the fact that our notion of aesthetic experience owes much to the thinking of 18th century European philosophers. It was then that craftwork and art, a distinction that had been growing since the Renaissance, were worked into clear-cut categories. The notion of artworks as autonomous objects that are free from functional purpose, that can be fully appreciated without reference to context, and that are intended solely for aesthetic contemplation was developed during the 18th century. This separation of art from other spheres of human experience, which is still a very commonly held view in Western countries but not among other cultures, was paralleled by the tearing of aesthetic interests away from all purpose and common pleasure (Carroll 2008). Art had traditionally been conceived as an integral aspect of people's social, moral, religious or recreational interests. After the 18th century, however, disinterested contemplation was considered to be the only appropriate way of approaching art (Kant 1790/1892): "(…) the shift from 'taste' to the 'aesthetic' came about partly as a result of giving a more intellectual character to the pleasures of the 'higher' senses of the eye and ear in order to further distance them from ordinary sensual enjoyments" (Shiner 2001 p. 141).

Nothing like the purposelessness and autonomy of art, espoused by the advocates of this modern system, existed before or in nonwestern societies. However, this new way of understanding art and aesthetic experience was never intended as a description of how all humans experience all art. The notion of disinterested aesthetic experience was elaborated to fit the philosophical paradigms and the social landscape that emerged throughout the 18th century, not to constitute a vehicle to study a sort of experience that is inherent to human nature.

Many scholars still regard aesthetic experience as a kind of disinterested contemplation of an object for its own sake. Carrol (2008) has argued that different versions of this view have remained influential due to its supporting role in understanding and accepting the Modern conception and classification of the arts: "To assure the autonomy of art from everything else, aesthetic experience is defined as something utterly apart from every conceivable purpose" (Carroll 2008, p. 152). Now, if neuroaesthetics aims to characterize the biological underpinnings of aesthetic experience—and we believe that most researchers would agree that all humans are capable of this kind of experiences by their very human nature—, then we must accept that a strict focus on the Western conception of aesthetic experience we have inherited, understood as a dispassionate, purposeless and decontextualized engagement, will never provide us with the whole story. In nonwestern societies the performance and enjoyment of art is often inextricably linked with rituals, ceremonies, celebrations and other events. Moreover, the associated experiences serve important economic, social, political and symbolic functions and purposes. Thus, nonwestern aesthetics generally permeates a broader range of activities and objects and is related with the communication of spiritual, ethical and philosophical meaning (Anderson 1989).

In sum, neuroaesthetics has inherited an excessively restrictive and maybe even inadequate concept of aesthetic experience to achieve its goals. In this sense, Carroll (2008) argued that "the standard characterization of aesthetic experience is effectively useless from the point of view of empirical research" (Carroll 2008, p. 158). If neuroaesthetics wishes to understand the biological bases of aesthetic experience, a particular form of experience afforded by our human nature, then it must be willing to account for varieties of such experience across many human cultures. In this case, however, the notion of aesthetics cannot "be regarded as pertaining to the study of the *visual* perception of the *beauty* of *a material object*" (Van Damme 1996, p. 56). If neuroaesthetics wishes to describe the *nature* of biological and psychological mechanisms underlying aesthetic experience, it requires a framework that is able to account for visual and auditory experiences, but also for olfactory, gustatory, tactile and kinesthetic experiences, as well as multiple and dynamic combinations of them. Moreover, it needs to account for perceptual experiences that are unrelated to beauty, such as those that arise from humans' engagement with the ugly, the comic, religious symbolism, identity markers, and so on (Van Damme 1996). And it needs to account for the physiological concomitants of experiences in which people show considerable degrees of interestedness, such as liking and disliking, wanting and rejecting, as well as the affective and emotional responses that accompany them. Hence, neuroaesthetics faces the challenge of developing a suitable framework that conceives aesthetic experience as a fully embodied and enactive experience. We are, in fact, faced with the same problem (Dewey 1934) set out to solve: "that of recovering the continuity of esthetic experience with normal processes of living" (Dewey 1934, p. 10).

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References

Alajouanine T (1948) Aphasia and artistic realization. Brain 71:229–241

Allen G (1877) Physiological aesthetics. Henry S. King & Co., London

Ambrose SH (2001) Paleolithic technology and human evolution. Science 291:1748–1753

Amunts K, Armstrong E, Malikovic A, Hömke L, Mohlberg H, Schleicher A, Zilles K (2007) Gender-specific left–right asymmetries in human visual cortex. J Neurosci 27:1356–1364

Anderson RL (1989) Art in small-scale societies, 2nd edn. Prentice Hall, Englewood Cliffs

Appenzeller T (1998) Art: evolution or revolution? Science 282:1451–1454

Azim E, Mobbs D, Jo B, Menon V, Reiss AL (2005) Sex differences in brain activation elicited by humor. Proc Natl Acad Sci USA 102:16496–16501

Baciu M, Koenig O, Vernier M-P, Bedoin N, Rubin C, Segebarth C (1999) Categorical and coordinate spatial relations: fMRI evidence for hemispheric specialization. NeuroReport 10:1373–1378

Bar M, Neta M (2007) Visual elements of subjective preference modulate amygdala activation. Neuropsychologia 45:2191–2200

Barton RA (2006) Primate brain evolution: integrating comparative, neurophysiological, and ethological data. Evol Anthropol 15:224–236

Bar-Yosef Mayer DE, Vandermeersch B, Bar-Yosef O (2009) Shells and ochre in Middle Paleolithic Qafzeh Cave, Israel: indications for modern behavior. J Hum Evol 56:307–314

Bäzner H, Hennerici M (2006) Stroke in painters. In: Rose FC (ed) The neurobiology of painting. Int Rev Neurobiol, vol 74. Academic Press, San Diego, pp 165–191

Bednarik RG (1995) Concept-mediated marking in the lower paleolithic. Curr Anthropol 36:605–634

Bednarik RG (2003) A figurine from the African Acheulian. Curr Anthropol 44:405–413

Bell EC, Willson MC, Wilman AH, Dave S, Silverstone PH (2006) Males and females differ in brain activation during cognitive tasks. Neuroimage 30:529–538

Berlyne DE (1963) Complexity and incongruity variables as determinants of exploratory choice and evaluative ratings. Can J Psychol 17:274–290

Berlyne DE (1970) Novelty, complexity, and hedonic value. Percept Psychophys 8:279–286

Berlyne DE (1971) Aesthetics and psychobiology. Appleton-Century-Crofts, New York

Berlyne DE, Ogilvie JC, Parham LCC (1968) The dimensionality of visual complexity, interestingness, and pleasingness. Can J Psychol 22:376–387

Berry JW (1968) Ecology, perceptual development and the Mueller-Lyer illusion. Brit J Psychol 59:205–210

Blood AJ, Zatorre RJ (2001) Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. Proc Natl Acad Sci USA 98:11818–11823

Blood AJ, Zatorre RJ, Bermudez P, Evans AC (1999) Emotional responses to pleasant and unpleasant music correlate with activity in paralimbic brain regions. Nat Neurosci 2:382–387

Boghi A, Rasetti R, Avidano F, Manzone C, Orsi L, D'Agata F, Caroppo P, Bergui M, Rocca P, Pulvirenti L, Bradac GB, Bogetto F, Mutani R, Mortara P (2006) The effect of gender on planning: an fMRI study using the Tower of London task. Neuroimage 33:999–1010

Bogousslavsky J (2005) Artistic creativity, style and brain disorders. Eur Neurol 54:103–111

Bogousslavsky J, Boller F (eds) (2005) Neurological disorders in famous artists. Frontiers of Neurology and Neuroscience, vol 19. Krager, Basel

Bouzouggar A, Barton N, Vanhaeren M, d'Errico F, Collcutt S, Higham T, Hodge E, Parfitt S, Rhodes E, Schwenninger J-L, Stringer C, Turner E, Ward S, Moutmir A, Stambouli A (2007) 82,000-year-old shell beads from North Africa and implications for the origins of modern human behaviour. Proc Natl Acad Sci USA 104:9964–9969

Bromberger B, Sternschein R, Widick P, Smith W II, Chatterjee A (2011) The right hemisphere in esthetic perception. Front Hum Neurosci 5:109. doi:110.3389/fnhum.2011.00109

Brown S, Martinez MJ, Parsons LM (2004) Passive music listening spontaneously engages limbic and paralimbic systems. NeuroReport 15:2033–2037

Bruner J (1983) In search of mind. Essays in autobiography. Harper and Row, New York

Bruner E, Manzi G, Arsuaga JL (2003) Encephalization and allometric trajectories in the genus *Homo*: evidence from the Neandertal and modern lineages. Proc Natl Acad Sci USA 100:15335–15340

Burke E (1757) A philosophical enquiry into the origin of our ideas of the sublime and the beautiful. Dodsley, London

Cahill L (2006) Why sex matters for neuroscience. Nat Rev Neurosci 7:477–484

Calvo-Merino B, Jola C, Glaser DE, Haggard P (2008) Towards a sensorimotor aesthetics of performing art. Conscious Cogn 17:911–922

Calvo-Merino B, Urgesi C, Orgs G, Aglioti SM, Haggard P (2010) Extrastriate body area underlies aesthetic evaluation of body stimuli. Exp Brain Res 204:447–456

Carroll N (2008) Aesthetic experience, art and artists. In: Shusterman R, Tomlin A (eds) Aesthetic experience. Routledge, New York, pp 145–165

Cela-Conde CJ, Ayala FJ (2007) Human evolution. Trails from the past. Oxford University Press, New York

Cela-Conde CJ, Marty G, Maestú F, Ortiz T, Munar E, Fernández A, Roca M, Rosselló J, Quesney F (2004) Activation of the prefrontal cortex in the human visual aesthetic perception. Proc Natl Acad Sci USA 101:6321–6325

Cela-Conde CJ, Ayala FJ, Munar E, Maestú F, Nadal M, Capó MA, del Río D, López-Ibor JJ, Ortiz T, Mirasso C, Marty G (2009) Sex-related similarities and differences in the neural correlates of beauty. Proc Natl Acad Sci USA 106:3847–3852

Cela-Conde CJ, Agnati L, Huston JP, Mora F, Nadal M (2011) The neural foundations of aesthetic appreciation. Prog Neurobiol 94:39–48

Chabris CF, Kosslyn SM (1998) How do the cerebral hemispheres contribute to encoding spatial relations? Curr Dir Psychol Sci 7:8–14

Changeux J-P (1994) Art and neuroscience. Leonardo 27:189–201

Chatterjee A (2004a) Prospects for a cognitive neuroscience of visual aesthetics. Bull Psychol Arts 4:55–60

Chatterjee A (2004b) The neuropsychology of visual artistic production. Neuropsychologia 42:1568–1583

Chatterjee A (2006) The neuropsychology of visual art: conferring capacity. Int Rev Neurobiol 74:39–49

Chatterjee A (2011) Neuroaesthetics: a coming of age story. J Cogn Neurosci 23:53–62

Chatterjee A, Widick P, Sternschein R, Smith WB II, Bromberger B (2010) The assessment of art attributes. Emp Stud Arts 28:207–222

Chatterjee A, Bromberger B, Smith WB II, Sternschein R, Widick P (2011) Artistic production following brain damage: a study of three artists. Leonardo 55:405–410

Cupchik GC (1986) A decade after Berlyne. New directions in experimental aesthetics. Poetics 15:345–369

Cupchik GC, Vartanian O, Crawley A, Mikulis DJ (2009) Viewing artworks: contributions of cognitive control and perceptual facilitation to aesthetic experience. Brain Cogn 70:84–91

d'Errico F, Henshilwood C, Vanhaerend M, van Niekerk K (2005) *Nassarius kraussianus* shell beads from Blombos Cave: evidence for symbolic behaviour in the Middle Stone Age. J Hum Evol 48:3–24

Davis CM (1970) Education and susceptibility to the Muller-Lyer illusion among the Banyankole. J Soc Psychol 82:25–34

Dewey J (1934) Art as experience. Minton, Balch and Company, New York

Di Dio C, Macaluso E, Rizzolatti G (2007) The golden beauty: brain response to classical and renaissance sculptures. PLoS ONE 11:e1201

Dupré E, Nathan M (1911) Le langage musical: Étude médico-psychologique. Maisons Félix Alcan et Guillaumin Réunies, Paris

Fechner GT (1865) Über die Frage des golden Schnitts. Archiv für die zeichnenden Künste 11:100–112

Fechner GT (1876) Vorschule der Ästhetik. Breitkopf und Härtel, Leipzig

Frumkin RM (1963) Sex, familiarity, and dogmatism as factors in painting preferences. Percept Motor Skill 17:12

Furnham A, Walker J (2001) The influence of personality traits, previous experience of art, and demographic variables on artistic preference. Pers Indiv Differ 31:997–1017

Gabora L (2005) Mind: What archaeology can tell us about the origins of human cognition. In: Bentley A, Maschner H (eds) Handbook of theories and methods in archaeology. Altamira Press, Walnut Creek, pp 283–296

Gosselin N, Peretz I, Johnsen E, Adolphs R (2007) Amygdala damage impairs emotion recognition from music. Neuropsychologia 45:236–244

Gourevitch G (1967) Un aphasique s'exprime par le dessin. Encephale 56:52–68

Green CD (1995) All that glitters: a review of psychological research on the aesthetics of the golden section. Perception 24:937–968

Haier RJ, Jung RE, Yeo RA, Head K, Alkire MT (2005) The neuroanatomy of general intelligence: sex matters. Neuroimage 25:320–327

Hugdahl K, Thomsen T, Ersland L (2006) Sex differences in visuo-spatial processing: an fMRI study of mental rotation. Neuropsychologia 44:1575–1583
Humphrey NK (1973) The illusion of beauty. Perception 2:429
Jacobsen T, Schubotz RI, Höfel L, von Cramon DY (2006) Brain correlates of aesthetic judgment of beauty. Neuroimage 29:276–285
Jager J, Postma A (2003) On the hemispheric specialization for categorical and coordinate spatial relations: a review of the current evidence. Neuropsychologia 41:504–515
Kant I (1790/1892) Critique of judgment. Macmillan and Co., London
Kawabata H, Zeki S (2004) Neural correlates of beauty. J Neurophysiol 91:1699–1705
Kirk U, Skov M, Christensen MS, Nygaard N (2009a) Brain correlates of aesthetic expertise: a parametric fMRI study. Brain Cogn 69:306–315
Kirk U, Skov M, Hulme O, Christensen MS, Zeki S (2009b) Modulation of aesthetic value by semantic context: an fMRI study. Neuroimage 44:1125–1132
Koelsch S, Fritz T, von Cramon DY, Müller K, Friederici AD (2006) Investigating emotion with music: an fMRI study. Hum Brain Mapp 27:239–250
Koffka K (1940) Problems in the psychology of art. In: Art: A Bryn Mawr symposium. Bryn Mawr Notes and monographs IX. Bryn Mawr College, Bryn Mawr, PA, pp 179–273
Kosslyn SM (1987) Seeing and imagining in the cerebral hemisphere: a computational approach. Psychol Rev 94:148–175
Kosslyn SM, Alpert NM, Thompson WL, Chabris CF, Rauch SL, Anderson AK (1994) Identifying objects seen from different viewpoints. A PET investigation. Brain 117:1055–1071
Leder H, Belke B, Oeberst A, Augustin D (2004) A model of aesthetic appreciation and aesthetic judgments. Br J Psychol 95:489–508
Lengger PG, Fischmeister FPS, Leder H, Bauer H (2007) Functional neuroanatomy of the perception of modern art: a DC-EEG study on the influence of stylistic information on aesthetic experience. Brain Res 1158:93–102
Lewis EO (1908) The effect of practice on the perception of the Müller-Lyer illusion. Br J Psychol 2:294–306
Luria AR, Tsvetkova LS, Futer DS (1965) Aphasia in a composer (V. G. Shebalin). J Neurol Sci 2:288–292
Marshack A (1996) A middle paleolithic symbolic composition from the Golan Heights: the earliest known depictive image. Curr Anthropol 37:357–365
Marshall HR (1892) The field of aesthetics psychologically considered II: the differentiation of aesthetics from hedonics. Mind 1:453–469
Marshall HR (1893) Hedonic aesthetics. Mind 2:15–41
Mellars P (2006) Why did modern human populations disperse from Africa ca. 60,000 years ago? A new model. Proc Natl Acad Sci USA 103:9381–9386
Miller G (2000) The mating mind. How sexual choice shaped the evolution of human nature. Doubleday, London
Miller GF (2001) Aesthetic fitness: how sexual selection shaped artistic virtuosity as a fitness indicator and aesthetic preferences as mate choice criteria. Bull Psychol Arts 2:20–25
Miller BL, Hou CE (2004) Portraits of artists. Emergence of visual creativity in dementia. Arch Neurol 61:842–844
Mitterschiffthaler MT, Fu CHY, Dalton JA, Andrew CM, Williams SCR (2007) A functional MRI study of happy and sad affective states induced by classical music. Hum Brain Mapp 28:1150–1162
Moore G (2002) Art and evolution: nietzsche's physiological aesthetics. Br J Hist Phil 10:109–126
Mountjoy PT (1958) Effects of exposure time and intertrial interval upon decrement to the Müller-Lyer illusion. J Exp Psychol 56:97–102
Nadal M, Pearce MT (2011) The copenhagen neuroaesthetics conference: prospects and pitfalls for an emerging field. Brain Cogn 76:172–183
Neisser U (1967) Cognitive psychology. Prentice Hall, Englewood Cliffs
Okubo M, Michimata C (2004) The role of high spatial frequencies in hemispheric processing of categorical and coordinate spatial relations. J Cogn Neurosci 16:1576–1582
Orban GA, Van Essen D, Vanduffel W (2004) Comparative mapping of higher visual areas in monkeys and humans. Trends Cogn Sci 8:315–324
Padovan R (1999) Proportion: science, philosophy, architecture. Taylor and Francis, London
Pedersen DM, Wheeler J (1983) The Müller-Lyer illusion among Navajos. J Soc Psychol 121:3–6
Piefke M, Weiss PH, Markowitsch HJ, Fink GR (2005) Gender differences in the functional neuroanatomy of emotional episodic autobiographical memory. Hum Brain Mapp 24:313–324
Pinter R, Anderson MM (1916) The Müller-Lyer illusion with children and adults. J Exp Psychol 1:200–221
Polzella DJ (2000) Differences in reactions to paintings by male and female college students. Percept Motor Skill 91:251–258
Preuss TM, Coleman GQ (2002) Human-specific organization of primary visual cortex: alternating compartments of dense Cat-301 and calbindin immunoreactivity in layer 4A. Cereb Cortex 12:671–691
Price U (1810) Essays on the picturesque, as compared with the sublime and the beautiful; and, on the use of studying pictures, for the purpose of improving real landscape, vol 1. J. Mawman, London
Ramachandran VS, Hirstein W (1999) The science of art: a neurological theory of aesthetic experience. J Conscious Stud 6:15–51
Salimpoor VN, Benovoy M, Larcher K, Dagher A, Zatorre RJ (2011) Anatomically distinct dopamine release during anticipation and experience of peak emotion to music. Nat Neurosci (in press). doi:10.1038/nn.2726
Schiano DJ, Jordan K (1990) Mueller-Lyer decrement: practice or prolonged inspection? Perception 19:307–316
Segall M, Campbell D, Herskovits MJ (1966) The influence of culture on visual perception. The Bobbs-Merrill Company, New York
Shiner L (2001) The invention of art: a cultural history. University of Chicago Press, Chicago
Shusterman R, Tomlin A (eds) (2008) Aesthetic experience. Routledge, New York
Silverman I, Eals M (1992) Sex differences in spatial abilities: evolutionary theory and data. In: Barkow J, Cosmides L, Tooby J (eds) The adapted mind. Oxford Univ Press, New York, pp 487–503
Silverman I, Choi J, Mackewn A, Fisher M, Moro J, Olshansky E (2000) Evolved mechanisms underlying way finding: further studies on the hunter-gatherer theory of spatial sex differences. Evol Hum Behav 21:201–213
Silverman I, Choi J, Peters M (2007) The hunter-gatherer theory of sex differences in spatial abilities: data from 40 countries. Arch Sex Behav 36:261–268
Skov M, Vartanian O (2009) Introduction: what is neuroaesthetics. In: Skov M, Vartanian O (eds) neuroaesthetics. Baywood, Amityville, pp 1–7
Souques A, Baruk H (1930) Autopsie d'un cas d'amusie (avec aphasie) chez un professeur de piano. Rev Neurol 1:545–556
Tatarkiewicz W (1963) Objectivity and subjectivity in the history of aesthetics. Phil Phenom Res 24:157–173
Terhune KP, Liu GT, Modestino EJ, Miki A, Sheth KN, Liu C-SJ, Bonhomme GR, Haselgrove JC (2005) Recognition of objects in

non-canonical views: a functional MRI study. J Neuro-Ophthalmol 25:273–279
Texier P-J, Porraz G, Parkington J, Rigaud J-P, Poggenpoel C, Miller C, Tribolo C, Cartwright C, Coudenneau A, Klein R, Steele T, Verna C (2010) A Howiesons Poort tradition of engraving ostrich eggshell containers dated to 60,000 years ago at Diepkloof Rock Shelter, South Africa. Proc Natl Acad Sci USA 107:6180–6185
Van Damme W (1996) Beauty in context. Towards an anthropological approach to aesthetics. Brill, Leiden
Vartanian O, Goel V (2004) Neuroanatomical correlates of aesthetic preference for paintings. NeuroReport 15:893–897
Webb D (1769) Observations on the correspondence between poetry and music. J. Williams, Dublin
Wertheimer M (1923) Untersuchungen zur Lehre von der Gestalt. II. Psychol Forsch 4:301–350
Yue X, Vessel EA, Biederman I (2007) The neural basis of scene preferences. NeuroReport 18:525–529
Zaidel DW (2005) Neuropsychology of art: neurological, cognitive, and evolutionary perspectives. Psychology Press, Hove
Zaidel DW (2010) Art and brain: insights from neuropsychology, biology and evolution. J Anat 216:177–183
Zaimov K, Kitov D, Kolev N (1969) Aphasie chez un peintre. Encephale 58:377–417
Zeising A (1854) Neue Lehre von den Proportionen des menschlichen Körpers. Rudolf Weigel, Leipzig
Zeising A (1855) Aesthetische Forschungen. Meidinger Gohn and Comp, Frankfurt am Main
Zeki S (1999) Inner vision. An exploration of art and the brain. Oxford University Press, Oxford
Zeki S (2001) Artistic creativity and the brain. Science 293:51–52
Zeki S (2004) The neurology of ambiguity. Conscious Cogn 13:173–196
Zeki S, Marini L (1998) Three cortical stages of colour processing in the human brain. Brain 121:1669–1685