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The beauty of the body

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Abstract Aesthetics can be defined as our ability to perceive, feel and sense objects in the world and assign them positive or negative values along a continuum between beauty and ugliness. The psychological processes underlying the sense of what is beautiful or ugly imply perception and appraisal of objects of art, as well as emotional and interoceptive reactivity towards them. Exploration of the neural underpinnings of these processes is at the core of neuroaesthetics, a new cognitive neuroscience domain that aims to investigate the neural activity associated with feelings of pleasure or displeasure generated by either cognitive or sensuous interaction with a wide variety of objects that may thus become objects of art. We argue that the sensuous dimension of art appreciation calls into play the cerebral sensorimotor representation of one's own and others' bodies. Studies indicate that specific brain areas process perception of static or dynamic bodies. In the present article, we discuss two related issues (1) whether aesthetic visual appreciation of bodies is based on neural activity linked to visual body perception, beauty appreciation or both and (2) whether there exists a single cerebral locus where all possible types of aesthetic experiences ultimately converge.

Keywords Neuroaesthetics · Body representations · Embodiment · Sensorimotor simulation

1 Introduction

1.1 Aesthetic perception and appreciation

Our interaction with environmental stimuli to which we attribute positive or negative qualities in the dimension of beauty or ugliness gives rise to aesthetic experience. This complex neuropsychological state implies the activation of perceptual–representational processes that cause sensations and feelings of pleasure or pain, attraction or repulsion, lust or fulfilment as well as cognitive processes that produce aesthetic attributions based on acquired knowledge about the art piece one physically perceives or art in general (Pihko et al. 2011). A variety of different entities (e.g. painting, sculpture, music, opera, theatre, literature, design and buildings as well as faces, bodies, flowers, landscapes, food) may be the object of aesthetic perception and appreciation. Philosophers and psychologists address the issue of why something is beautiful or ugly according to two main opposing perspectives. At one extreme they claim that beauty exists in the mind that contemplates things while at the other, they claim that perfect and universal forms of beauty (e.g. the so-called 'golden section' in abstract geometrical figures, McManus and Weatherby

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1997) do exist. Thus, while subjectivist theories posit that beauty 'is in the eye of the beholder' and is largely based on individual tastes and preferences possibly influenced by prior experience and cultural environment (Zajonc 1968), objectivist theories maintain that aesthetic experience depends on general qualities of the stimuli, such as, symmetry, balance, complexity, and order (Leder et al. 2004; Jacobsen et al. 2004). Yet, these two opposing views do not address the intrinsic phenomenological features of aesthetics, for example, stability (coherence) and modifications of individual's aesthetic appreciation during lifespan and social oscillations of taste.

Scholars have long acknowledged that aesthetic experience seems to be typically human, critically present in all cultures, defying barriers of class, race, and social status of individuals and is influenced by historical, evolutionary, and adaptive (e.g. the need to find suitable mates) variables (Jacobsen 2010). The strength and ubiquity of aesthetic appreciation in humans seems to indicate that this phenomenon has a communicative content in addition to its fundamental inmost dimension. Importantly, however, inter-individual differences in personality and in anatomic and physiological factors have attracted increasing attention in recent years. Aesthetic experience implies that viewing an appreciated object induces in the perceiving subject sensory, cognitive and affective gratification. Within this framework, it is important to investigate the extent to which the brain states of a given subject relate to the seemingly ineffable aesthetic properties of perceived objects.

2 Brainy aesthetics: the sense of beauty in a neural perspective

Although psychology has investigated the sense of beauty for decades, giving rise to the field of 'empirical aesthetics', only recently has neuroscience started to explore the neural activity underlying the human capacity to experience phenomena as aesthetic configurations and the neural activity at the basis of the human ability to create objects that evoke such aesthetic experience (Zeki 1999; Cela-Conde et al. 2004; Kawabata and Zeki 2004). Neuroaesthetics primarily focuses on the neural mechanisms linked to emotional appeal or to the capability of specific objects to disturb or arouse a person (Zeki 1999, 2001). Neuroaesthetic studies explore the brain processes underlying aesthetic perception, judgment, and evaluation of intrinsic perceptual properties of the stimulus (e.g., 'it is beautiful'), or of the observer's attitude towards the stimulus (e.g., 'I like it') (Jacobsen et al. 2006). Although the attempts to explain the neural underpinning of aesthetic experience use methodology and techniques peculiar to cognitive neuroscience, a variety of scholars from different disciplines including philosophers, art historians, artists, and psychologists are contributing to make the field of neuroaesthetics blossom. Over the last few decades, several studies investigated the neural activity induced by aesthetic appreciation through different sensory modalities (Brown et al. 2011; Cela-Conde et al. 2011). However, most of these studies concerned visual arts in the forms of paintings (Kawabata and Zeki 2004; Cela-Conde et al. 2004; Vartanian and Goel 2004), sculptures (Di Dio et al. 2007, 2011) and dance performances (Calvo-Merino et al. 2008; Cross et al. 2011). For example, in a functional magnetic resonance imaging (fMRI) study, subjects were asked to view portrait, landscape, still life or abstract composition paintings that they classified as beautiful, neutral, or ugly. The results showed that beautiful paintings elicited increased activity in the orbito-frontal cortex, which is involved in emotion and reward processes. Interestingly, the more ugly a painting, the greater the motor cortex activity, as if the brain was preparing the body to escape (Kawabata and Zeki 2004). A selective activation of the prefrontal area during the perception of objects qualified as beautiful has been reported in a magnetoencephalography study (Cela-Conde et al. 2004). A more complex pattern of decreased (right caudate nucleus) and increased (bilateral occipital gyri, left cingulate sulcus, and bilateral fusiform gyri) activation for decreased and increased preference of abstract paintings, respectively, was also reported (Vartanian and Goel 2004). These results support the link between aesthetic preference and reward systems and call for further studies on 'dopaminergic aesthetics' to explore the role of reward-system chemicals involved in modulating beauty appreciation.

In a more 'objectivistic' perspective, an fMRI study presented participants naïve to art criticism with images of classical and renaissance sculpture masterpieces either in their original version, based on the golden section proportion, or in a modified version that resulted from changes to the canonical torso/legs proportion (Di Dio et al. 2007). Cerebral activity was measured while participants performed three different tasks, namely, passive observation, proportion judgment and aesthetic judgment. The results of this study showed increased neural activity in the right insula during passive observation of the original sculptures relative to the modified ones, and in the right amygdala when the stimuli were rated more ugly than beautiful during the overt aesthetic judgment task. Based on this pattern of results, the authors speculated that the insula may be selectively involved in objective beauty representation while the amygdala may be more involved in subjective beauty experience (Di Dio et al. 2007). This interpretation may also suggest a functional link between the neural substrates supporting aesthetic evaluation and

appreciation of stimuli (e.g. insula) and the neural underpinnings involved in the attribution of cognitive or emotional value to perceived stimuli (e.g. caudate or amygdala).

In the following paragraphs, we discuss whether the appreciation of beauty relies upon special processes distinct from the appraisal of common objects and whether these processes are based on the many neural representations an observer constructs concerning an art object. In particular, we will address the issue of whether observing a sublime painting (e.g. depicting a body) is emotionally and cognitively distinct from perceiving non-art but still salient objects (e.g. a real human body).

3 The body in the brain

If we consider the human body as an object of aesthetic experience, it may help us instantiate, in neural terms, distinctive features of aesthetic appreciation including its inmost and intimate dimension and its interpersonal and communicative aspects. Bodies are 'trivially' made of flesh, blood and bone. However, they represent complex 'psychic objects' that mediate and implement very complex functions, from the notion of self to social interactions and negotiations. Thus, it is no surprise that specific brain regions in parietal, occipito-temporal, premotor, motor and somatic primary and secondary cortices as well as insular, cerebellar and subcortical brain regions are involved in body representations (Berlucchi and Aglioti 1997, 2010; Candidi et al. 2012). fMRI studies show that the visual perception of full bodies or body parts activates selective lateral (extrastriate body area, EBA) and medial occipito-temporal visual areas (fusiform body area, FBA) (Downing et al. 2001; Peelen and Downing 2005). Moreover, the causative influence of EBA activity on the ability to discriminate different bodies was demonstrated by transiently disrupting EBA activity via transcranial magnetic stimulation (TMS) in healthy individuals (Urgesi et al. 2004; Urgesi et al. 2007a; Pitcher et al. 2009) and by testing patients with selective lesions in body-specific brain areas (Moro et al. 2008). Although the surface of the body, its form and morphological details do indeed convey important beauty features (think for example of the saying "the beauty-is-only skin deep"), also other body features, such as movement and posture, can convey strong aesthetic information. Importantly, visual perception of the body recruits neural activity in somato-motor regions that may mediate the vicarious experience of what is observed in others and the embodiment of visual body features. In particular, matching proprioceptive, tactile, and nociceptive information coming from one's own body may benefit from the activity of neural regions dedicated to the visual processing of body images, which may in turn allow a direct matching between one's own and another's body and ultimately support the development of higher order social skills (Gallese 2003). Under normal circumstances, we are able to see our own body and its movements and to feel the associated somato-sensations. The coherent coupling of visual, somatomotor and interoceptive information is thought to be at the base of the feeling of being inside one's own body and being responsible for its movements.

We propose that studying the functions of body representations offers at least two possibilities to understand embodied beauty. The first comes from the notion that the nervous system contains several distinct body representations which may be impaired in clinical and subclinical conditions that alter the sense of bodily beauty (e.g. anorexia, apotemnophilia) and, secondly that we all have a body and feel within its physical borders. The second notion is linked to the possibility of testing whether the mechanisms of sensori- and somatomotor matching between observed and experienced states and the maintenance of the sense of embodiment are relevant to aesthetic appreciation.

4 Embodied beauty

The somatomotor instantiation of perceived bodies is at the very basis of 'embodying bodies' and of mapping onto ourselves what we see in others. As we will suggest in the current section, given the crucial sensorimotor dimension of aesthetic appreciation, embodiment phenomena may play a crucial role in attributing beauty to observed bodies and movements. Importantly, body representations are inherently plastic; they change according to culturally and developmentally driven transformations in cognitive and affective functions. Changes in body representations may thus encourage changes in perception and appreciation of the body's beauty. Studies indicate, for example, that non-body objects with a salient link to one's own body schema (e.g. rings, Aglioti et al. 1996; canes in blind people, Serino et al. 2007; racquets in expert tennis players, Fourkas et al. 2008) can become incorporated as part of the body schema itself. If an object may become part of one's own body, the question arises as to whether other entities toward which we may experience emotions, desires and aesthetic appreciation may also be embodied and therefore perceived as pertaining to the self. Aesthetic appreciation, particularly of art objects, may provide an interesting example. The feeling that an object pertains to exquisite art is reported as an ineffable cognitive and emotional experience. However, art appreciation has clear sensorimotor components and may be strongly embodied. The aesthetic experience of music, for example, elicits "shivers-down-the-spine" or

"chills" that parallel changes in heart rate, electromyogram, and respiration as well as changes in neural activity of several brain regions including the ventral striatum, nucleus accumbens, amygdala, orbitofrontal cortex, and ventral medial prefrontal cortex, which are associated with pleasurable reward, motivation, emotion, and arousal (Blood and Zatorre 2001; Salimpoor et al. 2011). Thus, exposure to artistic stimuli may profoundly influence the observer's bodily state via neural activations that are similar to those triggered by other sensorimotor states not directly associated to aesthetic appreciation. A clear example of this is the "Stendhal syndrome" characterized by heartbeat acceleration, dizziness, fainting, confusion and even hallucinations in response to exposure to art works (Magherini 2003). Interestingly, the syndrome, eponymously associated with the French writer (*Upon leaving Santa Croce, my heart was beating irregularly* (…), *life was ebbing out of me and I went onwards in fear of swooning*", Stendhal 1817) entails both mental (e.g. disturbances of the sense of reality described as feelings of strangeness or alienation), and physical (e.g. tachycardia, chest pains, weakness, sweating and sometimes stomach pains) components (Magherini 2003). Hence, perceiving the ineffable properties of art objects, be they paintings or pieces of music, may lead to changes in bodily feelings and in one's own sense of embodiment. A seemingly abstract entity, such as art, may thus provide the observer with extremely powerful bodily sensations that may even determine a psychophysical breakdown. On the one hand, such embodiment may derive from the inferred simulation of the artist somatomotor states (think for example about the theoretical manifesto underlying action painting, in which the creative process is associated with the painter's limb movements). On the other hand, embodying 'abstract' entities (the content of a painting, the state reached through meditation) may originate as a result of arbitrarily associated simulations that may cause painting perception to become linked to activity in brain regions initially unrelated to art appreciation.

Another example of altered multimodal sensory integration resulting in a temporally and spatially distorted embodiment is the case of the Italian painter Giorgio de Chirico. His paintings influenced the metaphysical movement of Surrealism and emphasize strange, eerie spaces, mainly set in Italian piazzas. Many of de Chirico's works evoke a sense of dislocation between past and present, between the individual subject and the space he or she inhabits. Although de Chirico is told to have suffered from migraines, Blanke and Landis (2003) discussed the possibility that de Chirico artistic production might instead have been influenced by morbid manifestations of temporal lobe epilepsy that may affect the function of the temporo-parietal junction, a crucial integrative region where bodily perceptions are matched with orientation in space and time. However, the contributing effects of neuropsychological disease on neuroaesthetics in artists' creativity is beyond the scope of the present article (see Zaidel 2010; Chatterjee 2011; Blanke and Landis 2003; Blanke and Pasqualini 2011 for very good review articles).

5 The beauty of the body

Explicit and, even more, implicit perception and appreciation of bodies along like/dislike aesthetic dimensions is a fundamental adaptive process. Crucially, the adaptive process was previously suggested to be the phylogenetic precursor of attractiveness and of beauty/ugly perceptive and perceptuo-affective dimensions (Thornhill and Gangestad 1999; Little et al. 2011). Facial beauty and attractiveness, for example, seem to have a crucial influence on mating preferences (Johnston 2006). Accordingly, high ratings of facial attractiveness parallel high goodness ratings supporting the Beauty-is-Good stereotype (Tsukiura and Cabeza 2011). Moreover, another person's high physical attractiveness is linked to a greater tendency to recognize another person's face as one's own after synchronous visuo-tactile stimulation of the two faces (i.e. enfacement illusion) (Sforza et al. 2010). Thus, aesthetic appreciation of physical bodies may enhance (or reduce) the tendency to "feel" and incorporate its visual features into ones' own body and self representations.

Although it is common sense that non-facial body parts and full body are also considered more or less attractive (e.g. consider the oscillations in history and cultures between preferences towards fat or thin bodies) and play a crucial role in mating behaviours, neuroscience research on body attractiveness is scarce. Extreme attitudes towards body preferences are strikingly evident in apotemnophilia, a particular clinical condition in the spectrum of body integrity identity disorders (Giummarra et al. 2011). In apotemnophilia, an altered body representation with seemingly normal brain functioning and an absence of signs of psychotic disease may induce: (1) the intense feeling that a normally functioning body part is intrusively and disturbingly placed into one's own body schema with the consequent desire to have it removed via amputation (xenomelia), and (2) a sexual attraction to amputees (acrotomophilia) as though 'aesthetic preference' for certain body morphology is driven by one's own body image (Ramachandran et al. 2009). Although research into this mysterious condition suggests that these patients suffer from right parietal lobe dysfunction (McGeoch et al. 2011), studies on aesthetic perception and appreciation as well as on symmetry judgments, particularly referred to the body, may cast new light on the cerebral representation of body beauty.

At any rate, whether and when the body may be considered an object of art is a different question, directly pertaining to neuroaesthetics. Indeed, the body is the elective medium of the expression of established forms of art ranging from dance to tattoos or body painting. Classical ballet, for example, in addition to sharing several features with other art forms, is uniquely expressed through body postures and complex, precise, and "beautiful" movements.

Although previous research on dance observation in experts (Calvo-Merino et al. 2005, 2006) or novices (Cross et al. 2006) focused on the action performed by a dancing body, two recent fMRI studies specifically focused on the beauty conveyed by a dancing body (Calvo-Merino et al. 2008; Cross et al. 2011). In the first study, participants watched dance stimuli and performed an irrelevant task. The beauty ratings of the stimuli were collected in a subsequent independent session. Bilateral brain regions in the occipital and in the right premotor cortex were more active during observation of stimuli considered to be more beautiful (Calvo-Merino et al. 2008). In the second study, brain activity was measured while participants observed dance stimuli and evaluated how much they liked the stimuli and how complex it would have been for them to replicate the depicted movements. Results showed that neural activity in occipito-temporal and parietal regions, which are also part of the action observation network, was higher for those stimuli rated as more beautiful and more difficult to reproduce (Cross et al. 2011). Overall, these two studies converge to suggest that, when bodies are involved, beauty appreciation is inherently sensorimotor in nature. Importantly, the ability to induce aesthetic appreciation in perceivers may also be linked to the innate ability to read another person's emotions via the observation of his/her body (de Gelder 2006; Tamietto and de Gelder 2010). Increasing attention has been recently given to the neural correlates of emotional processing for bodily postures and movements (Hadjikhani and de Gelder 2003; de Gelder et al. 2004: Tamietto et al. 2007; Grèzes et al. 2007). These studies converge in showing that the perception of others' emotional states via the observation of their body postures activates a number of emotion related (amygdalae, insula, nucleus accumbens, orbitofrontal cortex) and fronto-parieto-temporal cortical structures linked to action observation and motor response programming.

While fMRI may provide correlational evidence between changes in neural activity and a given mental phenomenon, non-invasive brain stimulation (e.g. repetitive TMS, rTMS) may highlight causal links between selective changes in brain functions and consequent changes in the behaviour or mental state under investigation (Pascual-Leone et al. 2000). We applied event-related rTMS to interfere with the neural activity of cortical regions known to be involved in visual body processing, namely, the ventral premotor cortex (vPMC) and the EBA (Urgesi et al. 2004, 2007a, b; Candidi et al. 2008; Moro et al. 2008). Interfering magnetic stimuli were delivered while participants rated which one of two body images they liked the most. The results indicate that virtual disruption of EBA reduced perceived beauty of the body stimuli while the opposite was true after disruption of vPMC.

6 A single neural locus for beauty and art?

As we discussed in the previous sections, several brain regions may be involved in aesthetic perception and appreciation of different objects or features of the same object. Accordingly, a recent fMRI study indicates that the neural signature underpinning hedonic response during aesthetic experience may be different for art sculptures and non-art biological stimuli like young athletes' bodies (Di Dio et al. 2011). In particular, appreciation of sculpture generated higher activation of the right antero-dorsal insula, suggesting that this region may play a specific role in aesthetic experience for artworks. In contrast, higher activity during appreciation of human bodies versus sculpture was found in the superior temporal sulcus (STS), a cortical region crucially involved in the perception of biological motion (Grossman et al. 2005), early response to desirable visual human stimuli (Ortigue et al. 2008) and in the perception of emotion conveyed by the body (Candidi et al. 2011). This result suggests that aesthetic perception and appreciation of body stimuli is stronger when they are perceived as realistic and natural and when it is easier to "embody" them via the activation of wider sensorimotor networks.

However, a unified biocultural theory of art raises the question of whether there exists a single neural locus responsible for the ineffable qualia of aesthetic experience independent from the specific object and sensory modality involved in the experience. This issue was examined in a recent, very comprehensive voxel-based meta-analysis of 93 neuroimaging studies of positive-valence aesthetic appraisal through vision, hearing, taste and smell (the sense of touch was left out because there were not enough studies to propose any reliable conclusion) (Brown et al. 2011). The results demonstrate that the right anterior insula is the only brain region consistently activated across all four modalities. The authors emphasize that the right anterior insula is involved in processing visceroautonomic emotions with a negative valence (e.g. disgust) particularly if they are mediated by olfactory and gustatory inputs. The authors suggest that the comparison between subjective interoceptive state and exteroceptive perception, which aims to determine whether perceived objects will satisfy or oppose

our homeostatic needs, may be primarily grounded in this region. The physiological role of the insula in matching environmental as well as interoceptive bodily information in order to regulate one's own homeostasis, together with an emotional evaluation of the stimuli occurring in the amygdalae, may fit with the notion that a given stimulus is coded aesthetically, regardless the modality of input. In addition, it is important to note that the right anterior insula seems inherently linked to the interoceptive awareness of body states (e.g. the ability to time one's own heart beat and to experience the sense of inner body). It can thus be argued that aesthetic processing may be fundamentally related to the assessment of whether a given stimulus is good or bad for the perceiver, together with a more basic emotional evaluation of a stimulus. In this perspective, it becomes clear why aesthetic appreciation may not be limited to artworks but may be extended to objects of survival advantage, such as food sources or any other object of potential pleasure. Thus, artworks do not activate emotion areas distinct from those involved in appraising everyday objects important for survival. In the same vein, pleasant scents or tastes will activate brain networks similar to those activated when seeing Caravaggio's paintings or listening to an Opera concert. However, things may be more complicated. Indeed, the notion of a general purpose circuit for pleasurable items seem contradicted by a study showing that art images activate concrete reward-related regions like the ventral striatum, hypothalamus and orbitofrontal cortex. Importantly, inter-areal connectivity analysis indicates that when observing art images and not when viewing non-art objects, activity in visual areas predicted activity in the ventral striatum (Lacey et al. 2011). This pattern of results suggests that visual art exerts a specific influence on the reward circuitry on the basis of the artistic features of a given object more than on its hedonic value (Lacey et al. 2011). Seemingly in search of a common neural locus for beauty appreciation is an fMRI study where participants rated the beauty degree of paintings and musical excerpts (Ishizu and Zeki 2011). Visual and acoustic stimuli were then classified as beautiful, indifferent or ugly. Several regions were activated during beauty appreciation, but an almost complete overlapping activity during the experience of musical and visual beauty was found only in the medial orbito-frontal cortex. Moreover, the activity in this region correlated with the subjective experience of beauty intensity. Although this cross-modal beauty mapping region is indeed related to reward circuitry (Ishizu and Zeki 2011), it is different from the one reported in the aforementioned meta-analysis by Brown et al. (2011). Thus, since at least two complex and separate regions may be responsible for the essence of aesthetic experience, the model of a single neural locus for beauty does not seem tenable. Indeed, in accordance with its complexity and variety, aesthetic experience may derive from joint activity of various cortical populations that are responsive to specific elementary or high order features characterizing the art pieces. A related open issue is whether each sensory system processes current information inflow based initially on sensory aesthetic evaluation and successively according to affective evaluation to achieve a final hedonic coding of the stimulus. A recent fMRI study comparing different cognitive strategies in the evaluation of images and the aesthetic content of visual stimuli, suggests that aesthetic experience is a function of the interaction between top-down orienting of attention (occurring in fronto-parietal regions) and bottom-up perceptual facilitation (in occipital and fusiform visual areas) (Cupchik et al. 2009). Although the emerging field of neuroculture (Chiao 2009; Frazzetto and Anker 2009) indicates that insular functions are shaped by cultural variables, little is know on whether this structure is involved in the appreciation of art through learning. Therefore, an important challenge for future studies in neuroaesthetics is to understand the dynamically configured neural networks that underlie 'natural' and culturally mediated subjective and objective sense of beauty.

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