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Neural Correlates of Aesthetic Experience in Art

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1. INTRODUCTION

The term aesthetics was coined by Baumgarten in XVIII century and originates from the Greek word *aisthese-aisthanomai*, meaning to perceive-feel-sense. In his work titled *Aesthetics* the domain of aesthetics is described as the sphere of sensibility: It relates to the knowledge of the world for how we can perceive it and ourselves as part of it.

In philosophy, the construct of aesthetics can be described according to two main positions. The Platonic position regards aesthetics as an objective construct, where beauty is strictly connected with the numerical-musical harmony that rules nature. According to Plato, beauty is to be searched into the objective qualities of objects, in measurable relations (i.e., proportions). The Kantian view, on the other hand, regards aesthetics and beauty as subjective, in that beauty is not a property of the *object* itself, but is has to be searched in the *subject*, the perceiver. Far to be relativistic, this view considers aesthetic judgment universal as well: In Kant's approach the "subject" is not the *individuus* and "subjective" is not a synonymous of arbitrary or relative. The subject's aesthetic judgment is universal if we interpret the word "subject" as the collection of the common human faculties of judging something as beautiful.

Although these two theoretical positions are divergent in their basic reflections about the nature of aesthetics, they both recognize crucial concepts: aesthetics is related to the beauty of things, embedded in nature and represented in art and, importantly, they both admit its universality. It is on the basis of these fundamental assumptions that science makes an attempt to clarify the nature of the human ability to value the beauty of things.

In the last decades, cognitive neuroscience has extended its field of investigation to the domain of aesthetics, focusing in particular on music and visual arts. The present thesis deals exclusively with the neuroscientific investigation of aesthetic experience in visual arts. The term currently employed to define this approach is *neuroesthetics*.

1.1 Art and the visual brain

The term neuroesthetics was coined by Semir Zeki referring to the study of the neural bases of beauty perception in art. Zeki's approach to art is closely related to the definition he provides for the functioning of the visual brain, namely a search for the constancies (unchanging properties) of objects, situations and so forth, with the aim of obtaining true knowledge about the world (Zeki, 1999). In this process, the brain (as the artist) needs to discard inessential information from the visual world in order to represent the real character of an object in an enduring manner. For instance, when defining colour constancy, the brain needs to discard information regarding the exact composition of the wavelength reflected by objects' surfaces; with dimension, inessential information is the precise visual distance; whereas, with form, it would be the exact viewing angle. It is in this selection process that the brain is able to retain and categorize never-changing information about a world that, on the other hand, is in continuous transformation. It is for their ability to capture the essential elements of the world that artists can be defined, according to Zeki, as "natural scientists" able to elicit an aesthetic response in the creative brain of the observer.

Another construal of aesthetic experience is that of the neurologist V.S. Ramachandran. Ramachandran's approach to neuroesthetics is concerned with the unfolding of "universal rules" that govern beauty perception in art. The description of these "universals" relates to the way in which visual perceptual rules can account for art processing in the observer. In particular, Ramachandran's theory rests on the interaction between cognition and physical pleasure, which is claimed to be rooted in the human biological makeup. Indian representations of the women's body, for example, often reflect attention to primordial elements that recall the idea of procreation, such as pronounced hips and breasts. This concept is accounted for by the “universal” of emphasis (Ramachandran and Hirstein, 1999).

As with Zeki’s approach, Ramachandran’s description of the artistic experience ultimately results in the pleasure gathered from the unfolding of perceptual elements that capture conceptual cores. For example, grouping, a perceptual process that allows the brain to extract a figure from the background, may be an enjoyable process. According to this perspective, perceptual grouping comes about as reinforcement to early vision at every stage of visual processing. The resolution of visual ambiguity would then result in a pleasant 'aha' experience accompanying the perceptual experience we make of the world. Artists’ skill would then hinge upon their ability to evoke these biological perceptual processes in the observer, who is urged upon a creative and pleasurable reconstruction of the observed artistic object.

The study of the brain as it responds to art implies the existence of neural mechanisms entailed in art appreciation that are common to all individuals. The elements that are able to elicit these neural processes, i.e. the “access keys”, though, may be various and variable. In fact, they are under the influence of cultural and experiential constraints that define fluctuating trends over time and across individuals, even within the same cultural frame. When we visit a museum or an art gallery, we do not simply perceive images, but we contemplate objects whose presence in that specific physical space is justified and determined by their status of artworks. Our fruition of art is certainly cognitively mediated, because the peculiar quality of our aesthetic experience is influenced by our personal culture, by the environment in which we were educated, by the aesthetic canons informing our time, by our level of expertise and familiarity with the artworks we contemplate. Both Zeki and Ramachandran’s approaches to neuroesthetics resolve this variability problem with the ability of the visual brain to process essential information from the world that remains immutable and that can most naturally find a biological access to the observers’ creative mind. Yet, the complexity of the relation that builds between an artwork and the observer compels us to reason beyond the mere, though vital, perceptual ability of the brain to capture essential elements from the environment.

The complexity associated with the studying of the neural bases underpinning aesthetic experience in the beholder is strongly reflected by the great heterogeneity across results from the related neuroscientific investigations. Resting with the idea that the aesthetic experience of a visual artwork begins with a visual analysis of the stimulus, we then need to recognize that it necessarily undergoes further levels of processing. Thus, one possibility for the heterogeneity observed across the results of the studies dealing with neuroesthetics is that they may reflect the output of different aesthetic processing levels (see Reber et al. 2004; Leder et al. 2004). Among these processing levels, some have been proposed, which include spatial coding (e.g., Cela Conde et al. 2009; Cupchik et al. 2009), motor mapping (Jacobsen et al, 2006; Freedberg and Gallese 2007), reward processes (Kawabata and Zeki 2004; Vartanian and Goel 2004; Lacey et al. 2011) and hedonic processes (Jacobsen et al. 2006; Di Dio et al. 2007, 2011; Cupchik et al. 2009; for a review, see Di Dio and Gallese 2009).

Taken together, the results of these studies characterize at least two main mechanisms underpinning the building up of an aesthetic experience. One is concerned with the motor encoding of the stimuli, supporting the embodied theory of aesthetic perception, and the other is concerned with the emotional dimension of the aesthetic experience. In the following sections I briefly describe evidence suggesting the brain mechanisms underpinning each of these processing levels.

1.2 Aesthetics and visuo-motor processing

A few studies have recently shown that aesthetic experience involves a spatial coding and motor mapping of the stimuli. Functionally, these processes are typically characterized by activation of parietal and premotor areas.

A recent study by Cela-Conde and colleagues (2009) investigated gender-related similarities and differences in the neural correlates of beauty using a set of images of either artistic paintings or natural objects, divided into 5 groups: abstract art; classic art; Impressionist art; Postimpressionist art; photographs of landscapes, artefacts, urban scenes and true-life depictions. Through magnetoencephalography (MEG), it was shown enhanced activation for “judged-beautiful” versus “judged-ugly” stimuli in several parietal foci, bilaterally for women and mainly in the right hemisphere for men, with a latency of just 300 ms after stimulus offset.

Activation of parietal areas during aesthetic experience was also shown in a recent fMRI study of Cupchik et al. (2009), in which participants viewed various categories of representational paintings (portraits, nudes, still-life and landscapes) that were classified as “hard-hedge” (containing well-defined forms) and as ”soft-edge” (containing ill-defined forms). The underling rationale for this classification was based on the hypothesis that “soft-edge” paintings, by virtue of their structure, should facilitate aesthetic experience by stimulating active image construction. Both “hard” and “soft”-edge paintings were presented in two conditions: one that required the participants to observe the images in an objective and detached manner to gather information about the content of the stimulus (pragmatic condition), and one that required the participants to observe the paintings in a subjective and engaged manner, appreciating the feelings evoked by the stimuli (aesthetic condition). Enhanced activation of the left superior parietal lobe was observed for the “soft-edge” paintings, particularly during the “aesthetic” condition.

Activation of parietal regions for aesthetic stimuli in these studies brings support to the idea that aesthetic experience is characterized by visuo-spatial coding as well as, importantly, by motor mapping. In fact, there is now consistent evidence coming from physiological and anatomical studies on macaque monkeys that the posterior parietal cortex, including the intraparietal regions, is part of the motor system, playing a fundamental role in visuo-motor transformations (for a review, see Fogassi and Luppino, 2005). In humans, as in monkeys, the posterior parietal cortex is involved in the organization and recognition of actions. It has been shown that posterior parietal areas map different motor acts (such as grasping) on the basis of the goal of the action (such as eating) of which they are a component (Fogassi et al., 2005). This functional organization, shared by the posterior parietal and ventral premotor areas, likely underpins high order cognitive functions, such as understanding others' basic motor intentions. These functions have been observed in the inferior parietal lobule (IPL) where visual information of ventral and dorsal stream is integrated with motor information, to build a pragmatic description of the observed object.

Involvement of parietal and premotor areas in aesthetic experience was further observed in the fMRI study of Jacobsen et al. (Jacobsen et al., 2006). Here, participants were required to make an aesthetic appraisal of abstract geometrical shapes, whose symmetry and level of complexity had been manipulated. Behaviourally, symmetry was shown to strongly affect aesthetic judgment, followed by stimulus complexity. The imaging results indicated that, in the comparison of symmetry judgment and aesthetic judgment tasks versus the control condition (observation of an arrow), activations were enhanced in areas subserving visuo-motor processes, including the intraparietal sulcus and the ventral premotor cortex, in both conditions (see also Study 1 and 2 below).

1.2.1 Aesthetics and Embodiment

Evidence supporting the involvement of motor processing during the aesthetic experience brings also support to the embodied theory of aesthetics, which is grounded on the sensori-motor component of perception. The biological mechanism upon which embodied theories of aesthetic experience rests is the mirror neurons mechanism. Mirror neurons are motor neurons originally discovered in the ventral premotor cortex of macaque monkeys (area F5) that discharge when the monkey executes goal-related hand motor acts, like grasping objects, and also when observing other individuals (monkeys or humans) executing similar acts. Neurons with similar properties were later discovered in a sector of the posterior parietal cortex reciprocally connected with area F5. Mirror neurons provide the neurophysiological basis for primates to recognize different actions made by other individuals: the same neural motor pattern characterizing a given motor act when actively executed is also evoked in the observer when witnessing the motor behaviour of others.

This matching mechanism has also been shown in humans. Empirical evidence further suggests that the same neural structures that are involved in the subjective experience of emotions and sensations are also active when we see others express the same emotions and sensations (Singer et al., 2004; for a review see Singer 2006). A whole range of different "mirror matching mechanisms" appears to be then present in the human brain. These mirror mechanisms have been interpreted as constituting a basic functional mechanism in social cognition, defined as embodied simulation (Gallese, 2011).

Since the activation of the mirror mechanism for action is typically induced by the observation of ongoing actions, its relevance for the aesthetic experience while contemplating static artworks could be negligible. However, even the observation of static images of actions leads to action simulation in the brain of the observer, through the activation of the same brain regions normally activated by execution of the observed actions (see, for example, Urgesi et al., 2006).

The significance of mirror neurons in understanding aesthetic responses to art has not been fully assessed. Freedberg and Gallese (2007) recently proposed that a fundamental element of aesthetic response to works of art consists of the activation of embodied mechanisms encompassing the simulation of actions, emotions, and corporeal sensations. Historically, theorists of art have commented on a variety of forms of felt bodily engagement with works of art, but the mechanisms by which this happens have remained unspecified or entirely speculative. Mirror mechanisms and embodied simulation can empirically ground the fundamental role of empathy in aesthetic experience. Freedberg and Gallese's theory of empathic responses to works of art is not purely introspective, intuitive or metaphysical, but has a precise and definable material basis in the brain/body system.

The sensory-motor or "cold" component of the mirror mechanism includes the activation of parietal and premotor areas, which have been often found active in neuroesthetic studies. The recent neuroimaging works by Di Dio and colleagues (see the experimental Studies 1 and 2), as well as the psychophysical studies by Di Dio et al. and by Massaro et al. (see Studies 3 and 4 below) provide suggestive evidence compatible with this hypothesis.

1.3 Aesthetics and emotions

In the studying of the mechanisms underpinning the pleasurable experience associated with aesthetics, it is important to distinguish between emotions arising by mere aesthetic pleasure and those resulting from aesthetic judgments. These two aspects pertain to processing levels of the aesthetic experience, which are tightly bound, yet not interchangeable. Whereas aesthetic pleasure is more concerned with an automatic hedonic response to artworks, aesthetic judgment requires the contribution of an explicit cognitive appraisal of the works of art, holistically grouping the individual's values, knowledge and personal taste, all factors that are influenced by cultural and experiential dynamics. Though separable, these two aspects are strongly related and continuously affect each other during the building up of the aesthetic experience.

1.3.1 Explicit appraisal and reward

The study of neuroesthetics has mostly dealt with aesthetic judgment, in that participants are typically asked to explicitly judge a visual stimulus either as beautiful or ugly. Kawabata and Zeki (2004), for example, used fMRI to investigate the neural correlates of beauty perception during the observation of different categories of paintings (landscapes, portraits, etc.) that were judged by participants beautiful, neutral or ugly. The core imaging results revealed different brain activations for judged-beautiful stimuli versus both neutral and ugly images in medial orbitofrontal cortex (OFC), an area typically associated with reward processes (see, for example, Schultz 2000). The differential activation observed in OFC consisted in decreased activity with respect to baseline, with judged-ugly stimuli evoking the lowest level of activation.

Similarly, Vartanian and Goel (2004) carried out an event-related fMRI study, in which explicit aesthetic preference for representational versus abstract paintings was investigated in 3 stimulus-versions: originals, altered, filtered. Participants indicated their preference with a button press at each stimulus presentation. Representational paintings evoked higher preference than abstract paintings. In both categories, original paintings elicited the highest preference. Brain imaging results showed decreased activation in caudate nucleus with decreasing preference for the observed paintings, suggesting that aesthetic experience also relies on areas involved in the processing of stimuli holding rewarding properties (Delgrado et al. 2000). Additionally, increasing preference for the presented paintings elicited increased activation in several areas, including the left anterior cingulate sulcus, an area known to be involved in reward-related processing of stimuli that vary in emotional valence (see Devinsky et al. 1995 for a review).

Additionally, a recent study by Lacey and colleagues (2011) showed that contrasting art vs. non-art material (matched for content) determined activation of reward-related areas, including ventral striatum and orbitofrontal cortex. These authors found that activation of reward-related areas was not associated with aesthetic preference ascribed to art images (as assessed post-scanning). Therefore, in contrast with the conclusions drawn from the above-cited studies, Lacey and colleagues proposed aesthetic appraisal of visual art to be related more to a general effect of the artistic status of the presented material rather than to its hedonic value.

Although alternative explanations have been put forward justifying activation of reward-related areas during art judgment, reward may be reasonably expected in aesthetic experience as the result of both emotional and higher order cognitive processes to reinforce behaviours that produce positive experiences (Kahnt et al. 2010). Evidence coming from clinical studies of ventro-medial prefrontal cortex lesioned patients strongly suggests that reward is a complex emotion arising at the interface with high order cognitive processes, such as those associated with counterfactual thinking and decision making (Camille et al. 2004). In particular, orbitofrontal cortex is shown to be involved in coding stimulus reward value and, in concert with the amygdala and ventral striatum, is implicated in representing predicted future reward, which is used to guide our choices toward the more rewarding option (Kahnt et al. 2010; for a review, see O’Doherty 2004).

In this respect, the “activation” of structures such as OFC reported in neuroesthetics researches could stem for the match between the expected value associated with the viewing of a beautiful object and the actual value associated with the presented stimuli. This process would then produce in the viewer a rewarding high-order emotion that endorses his/her positive behavioural response. This process is typically evoked by tasks such as those requiring judgments. Reward processes, thus, have to be distinguished from the emotions and sensations that characterize the hedonic aspect of an aesthetic experience, which relies on different processing mechanisms, as it will be fully discussed in the experimental studies to follow (see also Jacobsen et al. 2006; Cupchik et al. 2009).

1.3.2 The hedonic dimension of aesthetic experience

As discussed, the need to explicitly verify the volunteers’ subjective evaluations on experimental tasks inevitably leads to processes of self-evaluation and decision-making. In an experimental setting, though, these processes may interfere with the activation of those areas, which are involved in the more hedonistic aspect of the aesthetic experience. It is this particular feeling that defines, in our view, an aesthetic experience as such, distinguishing it from the more cognitive processes that accompany the aesthetic evaluation or judgment of an artwork. An aesthetic experience can be in fact regarded as one that allows the beholder to feel, sense the beauty of an artwork, ultimately producing pleasure. Importantly, this process should not require conscious evaluation, but should spontaneously arise in any suitable viewer by virtue of the intrinsic qualities of the vector, namely the artwork.

Borrowing from the Classical, and particularly Platonic, view this basic assumption, we conducted a series of studies aimed at unfolding, from a neuronal perspective, the hedonic dimension of an aesthetic experience. In particular, recent studies are described in the following chapter showing that the hedonic character of one’s aesthetic experience is underpinned by the activation of a brain network, which includes cortical areas encoding the physical properties of the stimuli and, crucially, the right anterior insula. Interestingly, the direct comparison between brain activations during the aesthetic judgment of art stimuli (Classical sculptures) and of biological non-art stimuli (photographs of young athletes) in our most recent fMRI study (Study 2 below) showed that the hedonic value of aesthetic experience hallmarked by insula activation is peculiar for artworks, distinguishing it from the aesthetic evaluation of non-art material.

The experimental studies composing the present thesis are fully described in the following chapter. These are divided into neuroimaging (*f*MRI) studies (Study 1 and 2) and into behavioural and eye-tracking studies (Study 3 and 4).

2. EXPERIMENTAL STUDIES

2.1 *f*MRI Studies

2.1.1 Study 1 - The golden beauty: brain response to Classical and Renaissance sculptures

One of the most debated issues in aesthetics is whether beauty may be defined by some objective parameters or whether it merely depends on subjective factors. The first perspective goes back to Plato's *objectivist view* of aesthetic perception, in which beauty is regarded as a property of an object that produces a pleasurable experience in any suitable viewer. This stance may be rephrased in biological terms by stating that human beings are endowed with species-specific mechanisms that resonate in response to certain parameters present in works of art. The alternative stance is that the viewers' evaluation of art is fully *subjective.* It is determined by experience and personal values (see Tatarkiewicz, 1970; Reber et al., 2004).

Although it is commonly accepted that subjective criteria play a major role in one's aesthetic experience (see Valentine, 1962), it is also reasonable to accept that there exist specific biologically-based principles which may facilitate the perception of beauty in the beholder. New artists, after all, typically first master the ability to represent standard principles of beauty, such as symmetry and proportion, and only then eventually bend these rules to represent their overall vision of the world (see Bayles and Orland, 2007).

In the present study we investigated the aesthetic effect of objective parameters in the works of art by studying brain activations (fMRI) in viewers naïve to art criticism who observed images of sculptures selected from masterpieces of Classical and Renaissance art that are commonly accepted as normative Western representations of beauty. An important feature that characterized the present study distinguishing it from others that also have attempted to clarify the neural correlates of aesthetic perception (Cela-Conde et al., 2004; Kawabata and Zeki, 2004; Vartanian and Goel, 2004; Jacobsen et al., 2006) was the use of two sets of stimuli that were identical in every aspects but one: proportion. More specifically, a parameter that is considered to represent the ideal beauty, namely the golden ratio (1:0.618; for reviews see Huntley, 1970; Livio, 2002), was modified to create a degraded aesthetic value of the same stimuli in a controlled fashion (Figure 1).

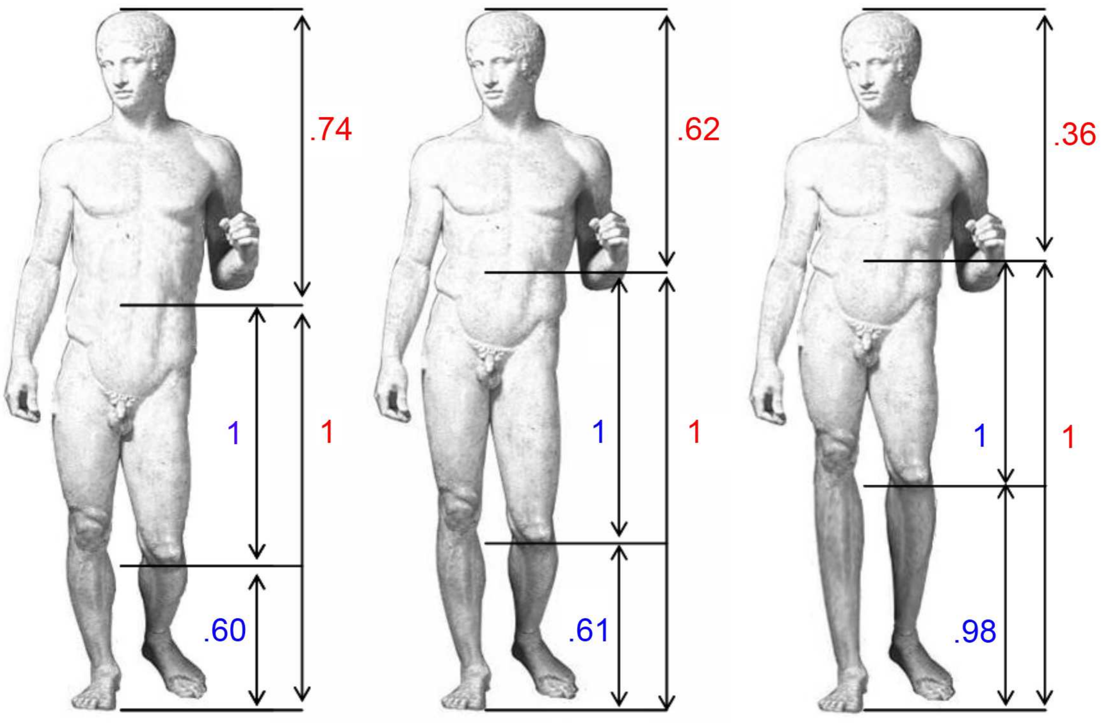

Figure 1. **Example of canonical and modified stimuli.** The original image (Doryphoros by Polykleitos) is shown at the centre of the figure. This sculpture obeys to canonical proportion (golden ratio = 1:1.618). Two modified versions of the same sculpture are presented on its left and right sides. The left image was modified by creating a short legs : long trunk relation (ratio = 1 : 0.74); the right image by creating the opposite relation pattern (ratio = 1 : 0.36). All images were used in behavioural testing. The central image (judged-as-beautiful on 100%) and left one (judged-as-ugly on 64%) were employed in the fMRI study.

Another important feature of the present study was that the same stimuli were presented in experimental conditions that varied in the instructions given to the viewers. In one condition - observation (O) – viewers were asked to observe the sculptures as if they were in a museum, without any explicit request to judge them. By inducing a “simply enjoy” contextual frame without having the volunteers perform any specific cognitive task, we meant to elicit a most spontaneous/unbiased brain response to the artworks. In a second -aesthetic judgment (AJ)- and third -proportion judgment (PJ)- condition, on the other hand, participants had to give an aesthetic or a proportion evaluation of the stimuli, respectively. They were involved therefore in an additional evaluation cognitive task. The aesthetic judgment condition allowed us to determine brain activations in response to the volunteer's subjective evaluation of the stimuli, whereas the PJ condition was used to observe brain response during a task of overt proportion evaluation.

In order to assess both "objective" and "subjective" aesthetic values, two types of analysis were carried out. In the first one, aimed to establish the neural responses to objective beauty parameters, we contrasted brain activations during the presentation of the canonical sculptures *vs*. their modified counterparts. The underlying rationale was that the canonical proportions intrinsic to the original works of art would elicit enhanced activity in areas mediating pleasure and, in particular, in the insula, the cortical region known to be involved in the *feeling* of emotion (see Damasio, 1999, 2000; Craig, 2003; Critchley et al., 2004, 2005). We also expected that signal increase would be particularly strong during the observation condition, where brain response to the artworks was not interfered with by additional cognitive requests (i.e. aesthetic or proportion judgment). The second type of analysis, on the other hand, was aimed at the evaluation of brain responses related to the overt subjective appreciation of the stimuli by contrasting the brain activations obtained during the presentation of the judged-as-beautiful against the judged-as-ugly images. In this analysis, we expected the judged-as-beautiful images to produce a stronger activation, than the judged-as-ugly images, in areas involved in the subjective emotional appraisal of the stimuli. In this case, however, we did not bring forward any specific prediction due to the divergent existing evidence in the field.

Experimental Procedure

Participants

Fourteen healthy right-handed volunteers (8 males, 6 females; mean age 24.5, range 12 years) participated in this study. They were educated undergraduate or graduate students, with no experience in art theory. After receiving an explanation of the experimental procedure, participants gave their written informed consent. The study was approved by the independent Ethics Committee of the Santa Lucia Foundation (Scientific Institute for Research Hospitalization and Health Care).

Stimuli

Fifteen 2-dimentional images of Classical and Renaissance sculptures were chosen following the selection method described in Supporting Information. All the original pictures met the criteria of canonical proportions defined by the ratio 1:1.618 between body parts; among the 15 modified image-versions, 7 presented a ‘long-trunk, short-legs’ modification (range = 1:1.47 - 1:1.59), whereas the remaining 8 images presented the opposite pattern of modification (range = 1:1.64 - 1:1.82). Twenty sculptures represented male bodies and 10 female bodies.

Paradigm

The stimuli were presented in three experimental conditions: observation (O), aesthetic judgment (AJ), and proportion judgment (PJ). Each participant underwent 6 separate fMRI runs, repeating each condition twice. The condition order was maintained fixed across all participants, with observation condition first, explicit aesthetic judgment second, and explicit proportion judgment, last. By keeping the observation runs first, we aimed at measuring unbiased (spontaneous) brain responses to the type of the stimuli (canonical and modified). To make sure that volunteers were not biased in their aesthetic judgment by explicit proportion evaluation, the aesthetic judgment condition always preceded the proportion judgment runs.

Within each run we presented 30 stimuli (15 canonical and 15 modified) in a randomized order, but never repeating the same image within a run. A question mark instructed the participants to respond to the images after a 4s-fix interval following each stimulus presentation by using a response box placed inside the scanner.

Task

Participants lay in the scanner in a dimly lit environment. The stimuli were presented on a black background and were displayed on a screen visible through a mirror mounted on the interior of the head coil. At the beginning of each session, a 5 s visual instruction informed the volunteers about the upcoming condition/task. On each trial, a 400ms central fixation point plus 1000ms blank-screen interval preceded the presentation of the sculpture stimulus. The stimulus then appeared at the centre of the screen for 2 s (see also Cela-Conde et al., 2004; Winkielman and Cacioppo, 2001) and it was followed by another 4 s blank-screen interval. After this, a question mark instructed the observer to respond to the stimulus (see below). The question mark remained on screen for 400 ms and was followed by a jittered interval ranging 2-5 s, with a uniform distribution.

During observation condition (O), the volunteers were required to observe the images as if they were in a museum and, when the question mark appeared, they had to indicate whether they paid attention to the picture or not. During the aesthetic and proportion judgment conditions, the volunteers were required to decide whether they liked the image (AJ) or whether they found it proportional (PJ), respectively. Thus, all 3 conditions required a response from the participants. Using the index or middle finger of the right hand, the participants answered yes or no, according to the instruction presented at the start of each run. Specifically, before the observation sessions, the participants were instructed to answer ‘yes’ if they paid attention to the stimulus just presented, whereas to press ‘no’ to indicate that they did not pay attention to the stimulus. The question ‘did you pay attention to the image?’ was introduced to make sure that participants were actually looking at the stimuli during fMRI scanning. During AJ condition, participants were required to indicate ‘yes’ if they aesthetically liked the image and ‘no’ if they did not. Finally, PJ condition required the observers to explicitly indicate whether they thought that the image was proportional by pressing ‘yes’ or if they thought that the image was disproportionate by pressing ‘no’.

The volunteers underwent six subsequent scanning runs, each lasting approximately 5.6 min. Each fMRI runs consisted of 30 trials with each sculpture images presented once.

Image acquisition

Functional images were acquired with a Magnetom Vision MRI scanner (Siemens, Erlangen, Germany) operating at 3T. Blood oxygenation level dependent (BOLD) contrast was obtained using echo-planar T2* weighted imaging (EPI). The acquisition of 32 transverse slices with an effective repetition time of 2.08 s, provided coverage of the whole cerebral cortex. The in-plane resolution was 3 x 3 mm.

Data analysis

Two types of analyses of fMRI data were performed. A stimulus-based analysis (‘objective beauty’) considered only the type of image that was presented to the participants: i.e. with canonical (C) or modified (M) proportions. The second analysis (‘subjective beauty’) categorized each sculpture image according to the behavioural responses measured during AJ runs. For this analysis, we included only images that were consistently judged either beautiful (B) or ugly (U) in both runs requiring aesthetic judgment.

Event-related fMRI data were processed with SPM2 (http://www.fil.ion.ucl.ac.uk). The first four image volumes of each run were discarded to allow for stabilization of longitudinal magnetization. For each participant, the remaining 162 volumes were realigned with the first volume, and the acquisition timing was corrected using the middle slice as reference (Henson et al., 1999). To allow inter-subject analysis, images were normalised to the Montreal Neurological Institute (MNI) standard space [18], using the mean of the 162 functional images. All images were smoothed using an isotropic Gaussian kernel (full width at half maximum = 10 mm).

Statistical inference was based on a random effects approach (Holmes and Friston, 1998). This comprised two steps. First, for each subject, the data were best-fitted (least-square fit) at every voxel using a linear combination of the effects of interest. The effects of interest were the timing of the fixation point onsets, the presentation times of the sculptures (C & M; or B & U), and the presentation times of the question mark that cued overt responses. All event-types were convolved with the SPM2 standard hemodynamic response function (HRF). Linear compounds (contrasts) were used to determine common effect (C+M *vs.* rest) and differential effects associated with the presentation of the sculptures (C-M and M-C; or B-U and U-B), separately for each of the three conditions (O, AJ and PJ). For each subject, this led to the creation of six contrast-images, that is three contrasts C+M *vs*. rest - - one for each condition, and three contrasts C-M *vs*. rest, again one for each condition. Additionally, three contrast-images were also created, which contrasted judged-as-beautiful *vs*. judged-as-ugly images for each condition.

These contrast-images then underwent the second step that comprised three separate ANOVAs. One considering overall pattern of activation ‘C+M *vs.* rest’ modelled for each condition; one considering ‘objective beauty’ (C *vs*. M) modelled for each condition; and one considering ‘subjective beauty’ (B *vs*. U) for each condition. Finally, for each of the three separate ANOVAs, linear compounds were used to compare these effects, now using between-subjects variance. Correction for non-sphericity (Worsley et al., 1996) was used to account for possible differences in error variance across conditions and any non-independent error terms for the repeated measures.

The following contrasts were tested. First, within the “common effects”, ANOVA (C+M *vs*. rest) averaging across all experimental conditions (O, AJ, PJ). For this, the SPM-maps were thresholded at *P*-corrected = 0.05 (voxel-level). The other two ANOVAs assessed any stimulus -specific effect (‘objective’: C-M, M-C; or ‘subjective’: B-U, U-B). We tested for main effects of stimulus across the three experimental conditions (O, AJ, PJ); and for interactions between stimulus and condition. Additional contrasts explored simple effects separately for the different conditions (e.g. B-U, during AJ only). For all these stimulus-specific effects, we used *P*-corrected = 0.05 at the cluster-level (cluster size estimated with a voxel-level threshold of *P*-uncorrected = 0.001, extent threshold = 10 voxels).

In addition, because of our prior hypothesis concerning the possible involvement of the insula in aesthetic appreciation, we used a small volume correction procedure to test for the effect of ‘objective beauty’ (C-M; within and across O/AJ/PJ conditions) specifically in this region. The search volume was derived from Damasio et al. (2000) (see also Critchley et al., 2005, 2005) centring a sphere at MNI x, y, z = 30, 18, 18; with a radius of 10mm.

Results and Discussion

The viewers’ evaluation of the stimuli, as expressed in the aesthetic judgment condition, showed that the canonical images were mostly evaluated positively (76%, sd= 0.18), whereas the modified images were generally scored with a negative rating (63%, sd= 0.25). This finding was in accord with a preliminary behavioural test used for images selection that also showed the relevance of proportion in aesthetic evaluation. In this test, violation of canonical proportions accounted for 77% of the variance in aesthetic rating (partial Eta^2; see Supporting Information in Di Dio et al., 2007 for details on the preliminary behavioural experiment).

Overall effect of viewing the sculptures

MRI analysis was carried out by first assessing the overall effect of viewing the sculptures contrasting canonical (C) and modified (M) images (pooled together, C+M) with rest, across all three conditions (O, AJ, PJ; *P*-corrected <0.05).

As shown in Figure 2, activations were found in occipital and temporal visual areas, including lingual and fusiform gyri. Additionally, activations were observed in the inferior parietal lobule (IPL) bilaterally, in the SMA/pre-SMA complex, ventral premotor areas, and in the posterior part of right inferior frontal gyrus (IFG). Signal increase was also found in the insula and hippocampus. Most of the activations were bilateral, although stronger in the right hemisphere. These results are summarized in Table 1 (see Appendix)**.**

Among the visual activations, besides the primary visual cortex, signal increase was found in the lateral occipital cortex and the inferior temporal lobe (shape sensitive areas), as well as in the MT/MST complex. This last finding, although surprising at first considering that the MT/MST complex is involved in the analysis of motion (Watson et al., 1993; Dupont et al., 1994; Orban et al., 1995), is consistent with previous data showing that activation of these areas may be elicited by static images that imply motion (Kourtzi and Kanwisher, 2000). Most noteworthy was the activation of the inferior parietal lobule and especially of the premotor cortex. These areas are known to become active during the observation of actions done by others (see Rizzolatti and Craighero, 2004). It is likely that their activation was dependent on the intrinsic dynamic properties of the sculptures used in this study and the sense of action that they evoked in the observer (see Freedberg and Gallese, 2007).

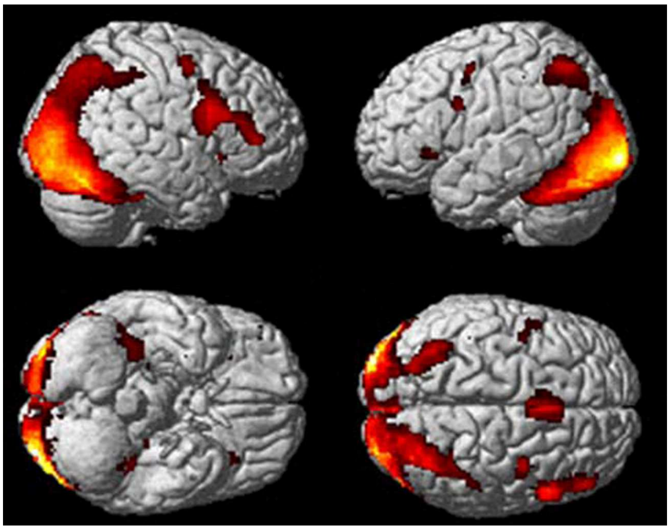

Figure 2. Brain activation of canonical and modified sculptures *vs.* rest. The analysis was carried out by averaging activity across the three experimental conditions (observation, aesthetic judgment, proportion judgment). Group-averaged statistical parametric maps are rendered onto the MNI brain template (*P*-corrected < 0.05).

Canonical vs. Modified Sculptures: "Objective Beauty"

The direct contrast of canonical *vs*. modified images across the three experimental conditions revealed signal increase for the canonical stimuli in the right occipital cortex extending into lingual gyrus; in the precuneus bilaterally; in the right posterior cingulate gyrus; and in the depth of right inferior frontal sulcus extending to the adjacent convexity of the middle frontal gyrus (*P*-corrected < 0.05; Figure 3a; see also Table 2a in Appendix).

The lateral occipital cortex (LOC, Malach et al., 1995; Grill-Spector et al., 2001) and the temporal visual areas are known to be responsive to the presentation of body parts or even the whole human body (Downing et al., 2001; Astafiev et al., 2005). Signal increase within these areas may be therefore due to a greater representation of canonical body structures relative to the disproportionate ones. The activation of the medial parietal areas and of the prefrontal lobe, on the other hand, might be related to mnemonic functions (e.g. Shallice et al., 1994; Tulving et al., 1994; for review see Cavanna and Trimble, 2006), possibly elicited by the retrieval of plausible motor configurations, better represented by the proportional material.

The central hypothesis underlying the present study was that the contrast of canonical *vs*. modified stimuli would produce signal enhancement within the insula. Accordingly, we carried out a small volume correction within the main effects analysis (C-M) using the anatomical coordinates reported in Damasio et al. (2000) on the feeling of emotion (see also Critchley et al., 2004, 2005). The results revealed a significant signal increase in the *anterior sector* of the right insular cortex extending to the operculum region (maxima x, y, z = 30, 26, 12; Figure 3b, $P < 0.05$, corrected for small volume).

This effect was particularly strong during *observation* condition ($P < 0.02$, corrected for the whole brain volume, see Table 2b in Appendix; $P = 0.005$, corrected for small volume), that is in the condition in which the volunteers were in a merely observational (museum-like) context (see Figure 3c). Signal increase in AJ and PJ conditions, on the other hand, was virtually the same. The most likely interpretation for this result stands in the different cognitive demands between the first (O) and the last two (AJ, PJ) conditions. In the latter, in fact, the explicit request of overtly judging the stimuli diverted the volunteers' attention resources towards a specific cognitive demand, thus lessening the natural neural response within the insula.

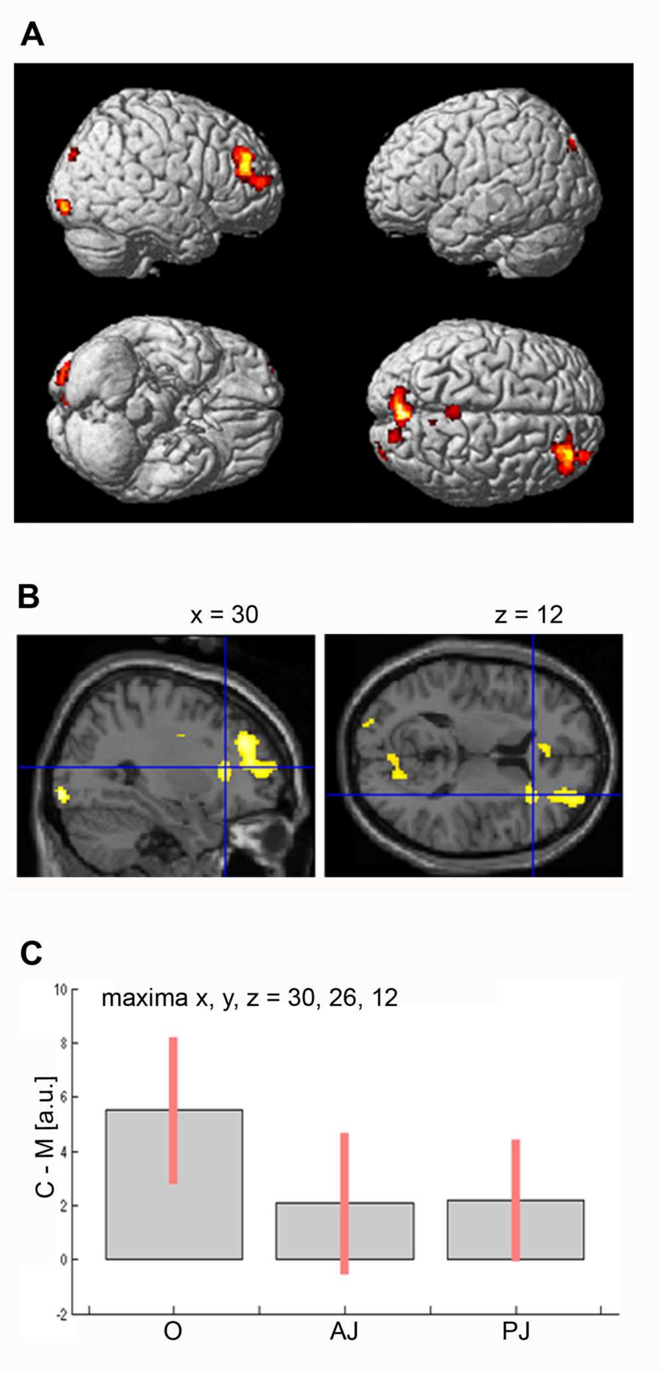

Figure 3. Brain activation in the contrast canonical *vs.* modified stimuli. A. Main effect of canonical *vs.* modified sculptures across conditions rendered onto the MNI brain template. **B.** Parasagittal and coronal view showing activations of the right insular region in the main effect. **C.** Activity profile of the right insula. For each condition (O, AJ, PJ) the signal plots show the difference between canonical (C) minus modified (M) sculptures in arbitrary units (a.u), +/- 10% confidence intervals (*P*-corrected < 0.05).

These data are in apparent contrast with some previous findings where symmetry was employed as an objective parameter of aesthetic evaluation (Jacobsen et al., 2006). In this study, the authors *did* find significant activation in the anterior insula in the comparison of aesthetic judgment *vs.* control condition as well as in symmetry judgment *vs.* control condition. However, they considered those areas that were activated by both aesthetic and symmetry judgment to be not involved in pure aesthetic judgment and hence omitted them from the analysis that directly contrasted brain activity for the judged-as-beautiful *vs.* the judged-as-ugly stimuli. In this way, therefore, they also disregarded the insular activation elicited by objective parameters (i.e. symmetry) intrinsic to the stimuli and involved in mediating the sense of beauty.

The question now arises of what possible mechanisms are responsible for the insula activation during the observation of canonical sculptures. The anterior sector of the insula has an agranular/disgranular cytoarchitectonic organization and is characterized by extensive connections with limbic structures and with centres involved in autonomic functions (Mesulam and Mufson, 1982, 1985; Dupont et al., 2003). Functionally, anterior insula is thought to mediate feelings associated with specific emotional states (Augustine, 1996, see Damasio, 1999, 2000; Craig, 2003; Critchley et al., 2004, 2005). Now, considering the pattern of activity described in the main effect (C+M *vs.* rest), there are two concurrent possibilities that may explain insula activation. One is that in LOC and in the parietal cortex there are neurons *specifically* sensitive to the canonical body images and that have privileged access to the insula. Alternatively, one may suppose that the canonical sculptures simply determined a *stronger* activation of cortical neurons sending their output to the insula.

Another possible explanation, based on both main and simple effect analyses (C-M), is that the insula was activated, not by simplest aspects of the visual stimuli (e.g. shape or motion), but rather by higher order information coming from prefrontal areas 45 and 46. Studies in primates (Nelissen et al., 2005) showed that area 45 integrates information about object shape with that about actions. While human left area 45 subserves language functions, it is plausible that human right area 45, selectively activated in the present experiment, could be involved in action/shape integration as well. In this light, canonical stimuli could be more efficiently coded in this area and determined, therefore, a stronger activation of the insula relative to the modified one. In this context, also the functional role of prefrontal area 46 could be noteworthy in confronting information from memory (e.g. standard body configuration) with online incoming information (observation of canonical and modified stimuli).

To summarize, we propose that the positive emotional *feeling* elicited in the viewer by the canonical images was determined by a preferential coding of these images, relative to the modified ones, by various cortical areas and by a concurrent, *joint* activation of the anterior insula.

Judged-as-Beautiful vs. Judged-as-Ugly Sculptures: "Subjective Beauty"

With this further analysis, we investigated the neuronal substrate associated with subjective appreciation of the sculptures as expressed by each participant in the AJ condition (2 runs). Behavioural data showed that 49% and 38% of stimuli were consistently judged, respectively, beautiful (B) and ugly (U) over both AJ runs, whereas 13% was rated inconsistently. Only the stimuli that were rated in a consistent way were employed for analysis.

The judged-as-beautiful images selectively activated the right amygdala. This effect was observed for the aesthetic judgment condition, as demonstrated by the stimulus x condition interaction analysis (maxima: x, y, z = 32, 2, -28; *P-corrected* < 0.03; Figure 4 a,b).

The amygdala is a complex nuclear structure. It is interconnected with several cortical areas and subcortical brain centres and subserves a variety of functional roles. However, a fundamental amygdalar function is to provide neutral stimuli with positive or negative values through association learning (e.g. LeDoux, 1996; Rotshtein et al., 2006; Phelps and LeDoux, 2005).

For a long time, studies involving the amygdala have mainly focused on negative stimulus conditioning. However, more recent studies support a role of the amygdala also for positive emotions, both in animals (Paton et al., 2006) and humans (e.g., Zald, 2003). This property puts the amygdala as a prime candidate in the storing of implicit emotional memories that can be subsequently accessed and used. In this light, the judged-as-beautiful stimuli could have been judged as such, not on the basis of their objective parameters, but because they were associated with memories charged with positive emotional values. The distinctiveness of each own experience would then partly explain the variance observed in the subjective rating of the observed images.

Finally, we compared judged-as-ugly versus judged-as-beautiful stimuli. As shown in Figure 4c, the only activated area was a region straddling the central sulcus (somatomotor cortices; P-corrected < 0.05; see also Table 3a in Appendix). Figure 4d shows signal change in this region, revealing a particularly strong effect of “ugly” versus “beautiful” images during the explicit aesthetic judgment condition. This selectivity was confirmed by the significant stimulus-by-condition interaction, as reported in Table 3 in Appendix.

These data are in accord with previous findings by Kawabata and Zeki (2004) showing that a negative evaluation of paintings (landscapes, abstract paintings, portraits, still life) determined the activation of the somatomotor region. There is also evidence from other studies that negative emotional stimuli may determine unilateral or bilateral activation in this region (e.g. fear, Armony and Dolan, 2002; anger, Zald, 2003; Dougherty et al., 2004).

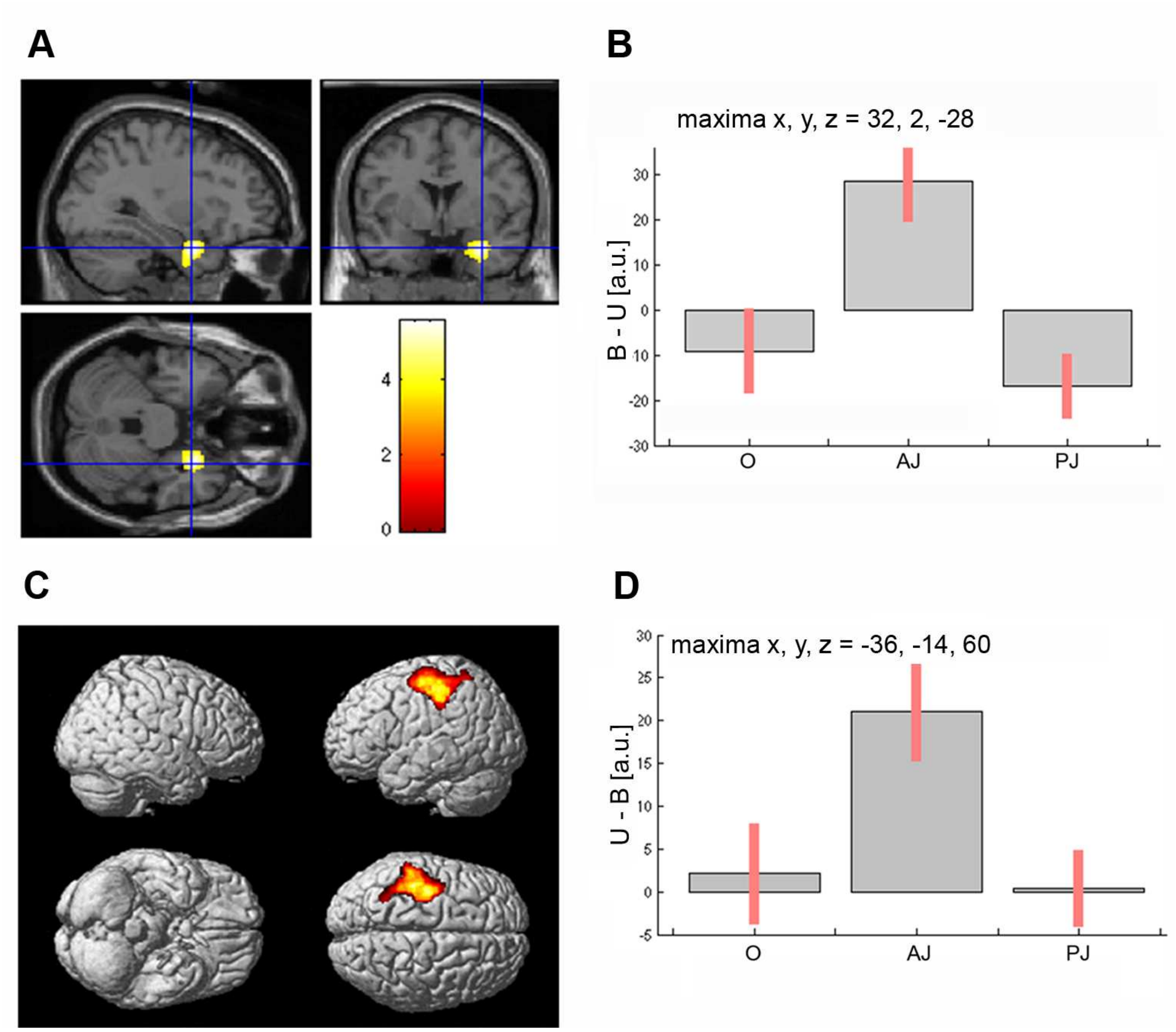

Figure 4. Brain activations in the contrasts "judged-as-beautiful *vs*. judged-as-ugly" and "judged-as-ugly *vs*. judged-as-beautiful" stimuli. a. Parasagittal, coronal and transaxial sections showing activation of the right amygdala in the interaction stimulus (beautiful *vs*. ugly) x condition (observation; aesthetic judgment; proportion judgment). **b.** Activity profile of the right amygdala. For each condition (O=observation, AJ=aesthetic judgment, PJ=proportion judgment) the signal plots show the difference between beautiful (B) minus ugly (U)-as judged sculptures in arbitrary units (a.u), +/- 10% confidence intervals. **c.** Statistical parametric maps rendered onto the MNI brain template showing activity within left somatomotor cortex in the contrast of ugly *vs.* beautiful stimuli averaged across the three conditions. **d.** Activity profile (ugly - beautiful) of the left motor cortex. For each condition (O, AJ, PJ) the signal plots show the difference between ugly (U) minus beautiful (B)-as judged sculptures in arbitrary units (a.u), +/- 10% confidence intervals (*P*-corrected < 0.05).

The activation of the somatomotor region during aesthetic judgment seems rather surprising in the absence of actual movements. However, this activation may find an explanation if one also considers the activity pattern (*deactivation*) of the orbito-frontal cortex reported in Kawabata and Zeki (2004) and also found in our work in a post-hoc analysis (see Supporting Information in Di

Dio et al., 2007). Although much attention has been drawn in recent years to the role of the orbito-frontal cortex in relation to positive rewards (for a review, see Rolls, 2000; Kringelbach, 2005), there is also evidence coming from lesion studies that damage to orbitofrontal cortex causes a liberation of a variety of behaviours, ranging from extreme irritability, hot temper, antisocial behaviour, to euphoria, locomotor hyperactivity and sexual disinhibition (e.g. Kleist, 1937; for a review see Boler and Grafman, 2001). If one admits that a decrease of activity in orbito-frontal cortex mimics - although to a different extent - the effect of a lesion, one may account for the motor activation in response to ugly stimuli as a covert release of an appropriate motor behaviour.

Concluding considerations

In the present study we addressed the issue of whether there is an objective beauty. Our results showed that objective parameters intrinsic to works of art are able to elicit a specific neural pattern underlying the sense of beauty in the observer. At the core of this pattern are neurons located in the anterior insula.

Insula mediates emotion *feelings*. It would be too reductive, however, to think that the sense of beauty occurs because of the activation of this structure alone. Insula is also activated by non-artistic stimuli; however, the feeling that these stimuli produce in the observer differs *qualitatively* from that determined by artworks. Our view is that this specific quality – the sense of beauty – derives from a *joint* activity of neural cortical populations responsive to specific elementary or high order features present in works of art and neurons located in emotion controlling centres.

The results of our analysis concerning what we called *subjective* beauty further revealed that, in the condition in which the viewers were asked to indicate explicitly which sculptures they liked, there was a strong increase in the activity of the amygdala, a structure that responds to emotional stimuli associated with one's own personal experiences and memories.

On the whole, the results of the present study suggest that both objective and subjective factors intervene in determining our appreciation of an artwork and that both processes are characterized by an emotional dimension.

2.1.2 Study 2 - Specificity of aesthetic experience for artworks: an fMRI study

In our previous study (Study 1) we investigated the neural correlates of aesthetic experience during the observation of masterpieces of Classical and Renaissance sculpture. In this study, sculpture images were presented to participants in two versions: original ("canonical") and proportion-modified. The rationale underlying proportion modification was that, in these masterpieces, proportion is strictly related to the aesthetic evaluation of the stimuli. By altering proportion in a controlled fashion and by keeping every other factors constant, it was then possible to unfold the neural correlates associated with the hedonic dimension of aesthetic experience for these artworks. Furthermore, in this study participants viewed the stimuli in three conditions: observation, aesthetic judgment and proportion judgment. The distinctive feature of this protocol was to allow participants, during observation condition, to observe the images without expressing any *explicit judgment*. In fact, explicit judgments that require decision-making may induce specific task-related processes that could diminish the neural activation responsible of hedonic responses.

The crucial contrast canonical *vs.* modified sculpture images in Study 1 revealed the activation of a brain network, which included cortical areas encoding the physical properties of the stimuli, areas encoding implied motion, and the right anterior insula. The emotional response, hallmarked by insula activation (Mesulam and Mufson, 1982, 1985; *Dupont et al.*, 2003; Augustine, 1996; Damasio, 1999, 2000; Craig, 2003, Chritchley, 2004, 2005) was particularly strong during observation condition, in which the participants could be said to respond most spontaneously to the presented images.

Support for the finding that the hedonic dimension of aesthetic experience is related to insular activation also comes from a recent study by Cupchik and colleagues (2009). In this *f*MRI study, participants viewed various categories of paintings (portraits, nudes, still-life and landscapes) that were presented in two conditions: one that required the participants to observe the images in an objective and detached manner to gather information about the content of the stimulus (“pragmatic condition”), and one that required them to observe the paintings in a subjective and engaged manner, appreciating the feelings evoked by the stimuli (“aesthetic condition”). Note that, similarly to our “observation” condition, instructions given to the participants prior “aesthetic” condition were to experience the mood evoked by the artworks without making any explicit judgment about the stimuli. The results of this study showed that observation of paintings under the “aesthetic” condition versus baseline condition (viewing of paintings accompanied by no explicit task-related instructions) elicited bilateral activation of the insula, suggesting that this area is crucially implicated in the hedonic feeling associated with aesthetic experience.

In the present study we investigated, using functional magnetic resonance imaging (*f*MRI), whether the hedonic response associated with aesthetic experience when viewing art masterpieces occurs also during the observation of non-art biological stimuli or whether it is distinctive of aesthetic experience for artworks. For this purpose, we compared the activations evoked by sculpture images with those produced by the observation of real human body images depicting young athletes. The athletes posed with body postures that resembled those portrayed in the sculpture images (for details, see Experimental Procedure section). In order to match the body configurations across stimulus-categories, all stimuli represented male figures (see Figure 1 for an example of stimuli).

This study was composed of two experiments. In both of them, we presented the two stimulus-categories (art *vs*. biological non-art) in two conditions: observation and explicit aesthetic judgment. The main difference between the two experiments laid in the stimulus presentation protocol and in the instruction provided to participants prior scanning. In Experiment 1, the stimuli (sculptures and real human body images) were presented intermixed in a semi-randomized order within the same functional runs. This protocol emphasized the differences between the two stimulus-categories. In Experiment 2, each stimulus-category was presented separately in different functional runs. By keeping the two stimulus-categories in separate runs we intended to highlight differences in brain activations distinctive of each stimulus-category.

The results showed a similar, yet not identical, activation pattern for the two stimulus-categories. The direct comparisons between sculpture and real human body images revealed differences at the visual and, most importantly, at the emotional level of processing. We argue that the activation pattern observed for sculptures images, inclusive of insula activation, pinpoints the hedonic aspect of aesthetic experience. This type of experience is lacking when viewing non-art biological stimuli.

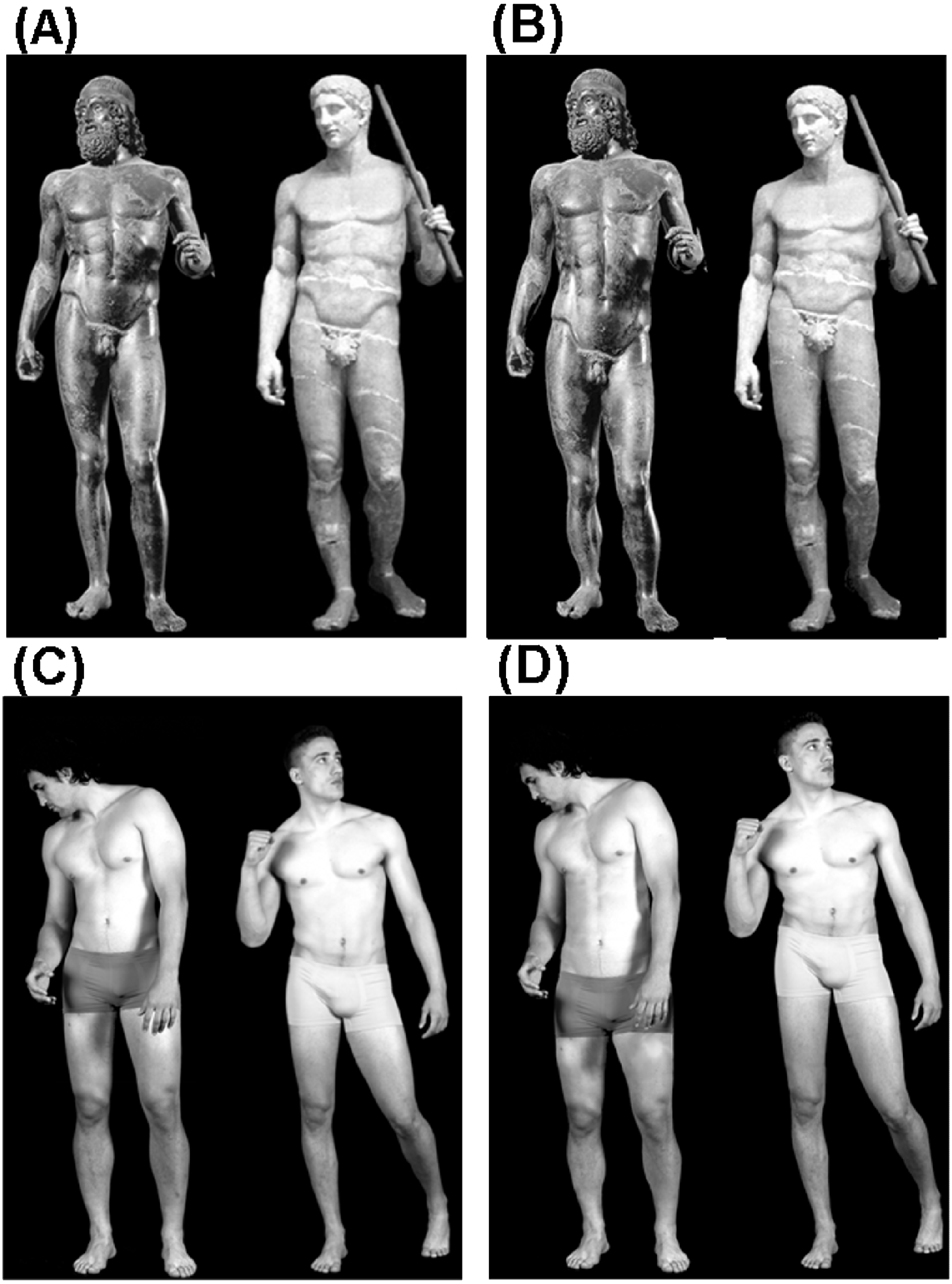

Figure 1. Example of experimental stimuli used in this study. **(A)** Images of canonical sculptures; **(B)** images of proportion modified sculptures; **(C)** images of canonical real human bodies; **(D)** images of proportion modified real human bodies. Proportion modified images (**B**; **D**) are presented with a long trunk-short legs relation (images on the left) and with a short trunk-long legs relation (images on the right).

Experimental Procedure

Participants

Thirty-two healthy right-handed Italian students (16 females [mean age=21.4, s.d.=1.23, range=19-25] and 16 males [mean age=23.43, s.d.=1.39, range=21-30]) participated in Experiment 1. Twenty-four healthy right-handed Italian students (12 females [mean age=20.28, s.d.=1.16, range=19-23] and 12 males [mean age=22.86, s.d.=3.26, range=19-30]) participated in Experiment 2. All participants were naïve to art criticism, as assessed during recruitment. They had normal or corrected-to-normal visual acuity. None reported a history of psychiatric or neurological disorders, or current use of any psychoactive medications. They gave their written informed consent to the experimental procedure, which was approved by the Ethics Committee of San Raffaele Scientific Institute (Milan) and Local Ethics Committee of Parma.

Stimuli

Sixteen 2-dimentional images of male sculptures (S) and 16 images of real male human bodies (HB) were chosen following the selection method described in Di Dio *et al.* (2007). For the present study, stimuli were selected out of an initial pool of images composed of a total 56 images of sculptures (28 canonical and 28 modified – see below) and 56 real human body images (28 canonical and 28 modified – see below). In this preliminary behavioural study, which was aimed at stimulus selection for the *f*MRI experiment, we examined the relation between aesthetic judgment and proportion in 22 observers naïve to art criticism. Participants of the behavioural study underwent observation, aesthetic judgment and proportion judgment conditions. To assess the probability that the stimuli were perceived either proportioned or disproportioned according to our prior categorization (canonical and modified), during proportion judgment, participants had to rate stimuli proportion on a dichotomous measure (0 – disproportioned; 1 – proportioned). During aesthetic judgment condition, on the other hand, participants had to rate the stimuli on a scale from 0 (ugly) to 7 (beautiful). By using a continuous scale, we aimed at increasing sensitivity on the assessment of the aesthetic response to the stimuli, which still needed to be quantified in this preliminary behavioural stage.

The original *canonical* images of sculptures were chosen from Classical examples that met the golden ratio criteria (proportion torso: legs (T-L) = 0.62 ± 0.01). The real body images were selected from pictures taken specifically for this study by a professional photographer using athletes, whose body proportion and figure resembled those portrayed in the sculpture images. Also the proportion associated with the selected real body images met the golden ratio criteria (proportion torso: legs (T-L) = 0.62 ± 0.02). Athletes were required to pose following the postures depicted in the sculpture images. All images were black and white and represented only male bodies that were comparable across categories in terms of body structure, proportion between body parts, posture, expressed dynamism. Expressed dynamism of the *canonical* sculpture and real body stimuli was assessed by 9 independent judges during the preliminary behavioural study aimed at stimulus selection (see above). The criteria according to which the evaluators assigned the stimuli to each category were the following: sense of balance, position of the limbs, feeling of motion, direction of eye-gaze and facial expression. Based on the judges' rating, stimuli were initially categorized into 10 dynamic and 18 static sculpture images and 12 dynamic and 16 static real body images. With respect to this further sub-categorization, the stimuli selected for the fMRI study contained an even number of judged-dynamic (8) and judged-static (8) images within each category.

A *modified* version of sculpture and real body images was created by altering the proportion between torso and legs (T-L) of the original images, thus producing two new sets of stimuli identical to the formers except for proportion. Using the algorithm employed in the previous experiment (Di Dio *et al.,* 2007), half of the images were modified by shortening the torso and elongating the legs (modification range T-L=0.5–0.6), whereas the other half followed the opposite modification pattern, with long torso and short legs (modification range T-L=0.64-0.75).

An example of the two stimulus-categories (original and modified) is in Figure 1.

Paradigm and Task Experiment 1

The stimuli were presented in a 2x2 design, with two levels of stimulus-category [sculpture (S) and real human body (HB)] and two levels of stimulus-type [canonical (C) and modified (M)]. The stimuli were presented in two separate experimental conditions [observation (O) and aesthetic judgment (AJ)]. Each participant underwent 8 separate *f*MRI runs, repeating each experimental condition twice. The condition order was maintained fixed across all participants, with observation condition first (runs 1-4), and explicit aesthetic judgment last (runs 5-8). By keeping the observation runs first, we aimed at measuring unbiased (spontaneous) brain responses to the stimuli. The participants expressed their explicit aesthetic judgment during the aesthetic judgment condition.

Every run comprised 32 trials. Sculpture images were presented in sixteen trials, and real human bodies images were presented in the other 16. Within each category-specific trials, half of the images (8) were presented in the canonical version and half (8) in the modified version. To reduce possible cross-category carry-over cognitive effects, stimuli were presented in a semi-randomized order, with mini-blocks consisting of 8 consecutive images of the same stimulus category (either S or HB), never repeating the same image within a run.

Participants lay in the scanner in a dimly lit environment. The stimuli were viewed via a back-projection screen located in front of the scanner and a mirror placed on the head-coil. The software Presentation 11.0 (Neurobehavioral systems, Albany, CA, http://www.neurobs.com) was used both for stimuli presentation and for the recording of the participants' answers. At the beginning of each run, a 4s visual instruction informed the participants about the upcoming condition. On each trial, the stimulus appeared at the centre of the screen for 2.5s and was followed by a 3s blank-screen interval. Subsequently, a question mark instructed the participants to respond to the stimulus in accordance with the task introduced (see below). The question mark remained on screen for 400ms and was followed by an Inter-Stimulus Interval (ISI; white-cross fixation) whose duration was varied ("jittered") at every trial, in order to desynchronize the timings of event-types with respect to the acquisition of single slices within functional volumes and to optimize statistical efficiency (Dale, 1999). The OptSeq2 Toolbox (http://surfer.nmr.mgh.harvard.edu/optseq/) was used to estimate the optimal ISIs (mean ISI = 3.87s, range = 1.5-19.750s). Each scanning run lasted approximately 6.5min.

During observation condition (O), the participants were required to simply observe the images and, when the question mark appeared, they had to indicate whether they paid attention to the image or not. During the aesthetic judgment condition, they were required to decide whether they aesthetically liked the image or not. Thus, both conditions required a response from the participants. Using the index or middle finger of the right hand, the participants answered yes or no, according to the instruction presented at the start of each run. The question 'did you pay attention to the image?' was introduced to make sure that participants were actually looking at the stimuli during *f*MRI scanning.

Paradigm Experiment 2

Participants lay in the scanner in a dimly lit environment. The stimuli were viewed via digital visors (VisuaSTIM) with a 500,000 px x 0.25 square inch resolution and horizontal eye field of 30°. The visors were applied directly on the volunteers' face. The digital transmission of the signal to the scanner was via optic fiber. The software E-Prime 2 Professional (Psychology Software Tools, Inc., Pittsburgh, USA, http://www.pstnet.com) was used both for stimulus presentation and recording of the participants' answers.

The structure of the experimental trials within each run was identical to that described for Experiment 1. Differently from Experiment 1, in Experiment 2 the total duration time of each run doubled (about 12 minutes), making 4 the total number of functional runs. However, the actual main difference with Experiment 1 laid in how stimuli were presented. In Experiment 1, stimuli presentation was organized in randomized mini-blocks of 8 stimuli belonging to the same category (either S or HB). In Experiment 2, instead, half of the participants (N=13) were presented with all sculpture images first (runs 1-2) and then with real human body images (runs 3-4), and half of the participants were presented with the opposite order. In this way, instructions for each experimental condition (particularly for observation condition, where we aimed at priming the proper mind-state) could be addressed more precisely in accordance with the specific stimulus category to follow. More specifically, during observation condition of sculpture images the volunteers were required to observe the images as "they were in a museum". During observation condition of real human bodies, they had to observe images "as if leafing through a magazine where they would have seen boys posing for photograph shots". For both stimulus-categories, participants were instructed to relax and observe the stimuli trying to explore each image in full.

fMRI data acquisition

For Experiment 1, anatomical T1-weighted and functional T2*-weighted MR images were acquired with a 3 Tesla Philips Achieva scanner (Philips Medical Systems, Best, NL), using an 8-channels Sense head coil (sense reduction factor=2). Functional images were acquired using a T2*-weighted gradient-echo, echo-planar (EPI) pulse sequence (38 interleaved transverse slices covering the whole brain with the exception of the primary visual cortex and the posterior part of the cerebellum, TR=3000ms, TE=30ms, flip-angle=85 degrees, FOV=240mm x 240mm, inter-slice gap=0.5mm, slice thickness=4mm, in-plane resolution 2.5mm x 2.5mm). Each scanning sequence comprised 120 sequential volumes. Immediately after the functional scanning a high-resolution T1-weighted anatomical scan (150 slices, TR = 600 ms, TE = 20 ms, slice thickness = 1 mm, in-plane resolution 1 mm x 1 mm) was acquired for each participant.

For Experiment 2, anatomical T1-weighted and functional T2*-weighted MR images were acquired with a 3 Tesla General Electrics scanner equipped with an 8-channels receiver head-coil. Functional images were acquired using a T2*-weighted gradient-echo, echo-planar (EPI) pulse sequence (acceleration factor asset 2, 37 interleaved transverse slices covering the whole brain, TR=2100ms, TE=30ms, flip-angle=90 degrees, FOV=205mm x 205mm, inter-slice gap=0.5mm, slice thickness=3mm, in-plane resolution 2.5mm x 2.5mm). Each scanning sequence comprised 306 sequential volumes. Immediately after the functional scanning a high-resolution inversion recovery prepared T1-weighted anatomical scan (acceleration factor arc 2, 156 sagittal slices, matrix 256x256, isotropic resolution 1x1x1 mm^3, TI=450ms, TR=8100ms, TE=3.2ms, flip angle 12°) was acquired for each participant.

fMRI statistical analysis

Image pre-processing and statistical analysis were performed using SPM8 (Wellcome Department of Cognitive Neurology, http://www.fil.ion.ucl.ac.uk/spm), implemented in Matlab v7.6 (Mathworks, Inc., Sherborn, MA) (Worsley and Friston, 1995). The first 6 volumes (Experiment 1) and the first 4 volumes (Experiment 2) of each functional run were discarded to allow for T1 equilibration effects. All remaining volumes from each participant were then spatially realigned (Friston *et al.*, 1996) to the first volume of the first run to correct for between-scan motion, and unwarped (Andersson *et al.*, 2001). A mean-image from the realigned volumes was created. The T1-weighted anatomical image was coregistered to such mean-image, and segmented in grey matter, white matter and cerebro-spinal-fluid. During the segmentation the grey-matter component was automatically normalized to a grey-matter probabilistic map (http://Loni.ucla.edu/ICBM/ICBM_TissueProb.html). The derived spatial transformations were then applied to the realigned-and-unwarped T2*-weighted volumes, that were resampled in 2x2x2 mm^3 voxels after normalization. All functional volumes were then spatially smoothed with an 8-mm full-width half-maximum (FWHM) isotropic Gaussian kernel to compensate for residual between-subject variability after spatial normalization.

Statistical inference was based on a random-effects approach (Friston *et al*., 1999). This comprised two steps. At the first (single-subject) level, *f*MRI responses were modelled in a design-matrix comprising the onset-times of the following regressors: instruction, stimuli (S and HB; C and M), blank intervals and question-mark that cued overt responses. Regressors modelling events were convolved with a canonical Haemodynamic Response Function (HRF), and parameter estimates for all regressors were obtained at each voxel by maximum-likelihood estimation. Linear contrasts were used to determine a) common effects (sculpture *vs*. baseline and real human body images *vs*. baseline, for both canonical and modified image types within each stimulus category), and b) differential effects associated with the presentation of the sculptures (C-M and M-C) and of the real human body images (C-M and M-C), separately for each of the two conditions (O and AJ). Finally, differential effects were also observed across stimulus categories, contrasting the effects evoked by sculpture images *vs*. real human body images (and vice-versa) within each experimental condition. For each participant, this led to the creation of 11 contrast-images in Experiment 1, that is one for each of the sub-conditions (2x2: stimulus-type x stimulus-category) for each experimental condition (O and AJ) plus 3 common to all conditions (instruction, blank interval and motor response); and of 10 contrast-images in Experiment 2, that is one of each of the sub-conditions (2x2: stimulus-type x stimulus-category) plus 2 common to all conditions (blank interval and motor response – see below).

These contrast-images then underwent the second step where the regressors of interest were modelled into Flexible Factorial analyses. The models considered the pattern of activation of the two stimulus types (C and M) *vs*. implicit-baseline for each of the 2 stimulus categories (S and HB) for each condition (O and AJ) Linear contrasts were used to compare these effects. Correction for non-sphericity (Friston et al., 2002) was used to account for possible differences in error variance across conditions and any non-independent error terms for the repeated measures.

Within the Flexible Factorial analyses, the following contrasts were tested. First, the “common effects of stimulus-category” (S, C+M *vs*. baseline) and (HB, C+M *vs*. baseline) averaging across the two experimental conditions (O and AJ). Second, contrasts explored main and simple effects of stimulus category comparing activations in response to canonical sculpture *vs.* canonical real human stimuli (SC *vs*. HBC and vice versa) across and within the two experimental conditions (O, AJ). Finally, every stimulus–type (canonical *vs*. modified) specific effect was assessed within stimulus-category (‘S’: C *vs.* M, M *vs.* C; ‘HB’: C *vs.* M, M *vs.* C) separately for each condition (O, AJ).

In order to analyze only activations above baseline, all contrast analyses (in both Experiment 1 and 2) were masked inclusively for the effect under investigation (e.g., for the contrast SC-HBC during AJ, the contrast was masked inclusively by SC_AJ). Results were thresholded at $P<0.05$ FWE corrected at the cluster or voxel level (cluster size estimated with a voxel-level threshold of *P*-uncorrected = 0.001).

The location of the activation foci was determined in the stereotaxic space of MNI coordinates system. Those cerebral regions for which maps are provided were also localized with reference to cytoarchitectonical probabilistic maps of the human brain, using the SPM-Anatomy toolbox v1.7 (Eickhoff et al, 2005).

Results

Behavioural results

Behavioural data analysis was carried out on the basis of participants' responses during AJ scanning sessions. Responses were dichotomous (see Methods section). Since each stimulus was repeated twice, only responses that were consistent between repetitions were used for analysis. Overall, most of the responses were congruent between repetitions (% of congruence Experiment 1: SC=95, SM=93, HBC=92, HBM=92; % of congruence Experiment 2: SC=95, SM=93, HBC=92, HBM=92).

A 2x2 repeated measures GLM analysis with 2 levels of stimulus-category (S *vs*. HB) and two levels of stimulus-type (C *vs*. M) was carried out considering the percentage of judged-as-beautiful responses ascribed to each stimulus type/category. On the whole, data obtained from the fMRI behavioural responses from Experiment 1 showed a main effect of stimulus-category [S>HB; (F(1,30)=4.29, p=.047, partial η^2=.13, power=.52)] as well as a main effect of stimulus-type [C>M; (F(1,30)=18.22, p<.001, partial η^2=.39, power=.99)]. Results from Experiment 2, showed only a main effect of stimulus-type [C>M; (F(1,17)=21.14, p<.001, partial η^2=.55, power=.99)] and no significant difference in aesthetic rating across categories (p>0.05).

fMRI results

Experiment 1

Overall effect of viewing sculpture and real human body images

In the first *f*MRI analysis, we assessed, separately, the overall effect of viewing the *sculpture* (S) and *the real human body* (HB) images. In both cases, we pooled together brain activations in response to canonical (C) and modified (M) images across the two conditions (observation and aesthetic judgment) and contrasted them with implicit baseline.

With respect to sculpture images, BOLD signal increase was found in the occipital lobe, inferior and middle temporal lobe, inferior parietal lobule (IPL/Intraparietal Sulcus), pre-SMA, ventral premotor cortex, and in inferior frontal gyrus (IFG). Signal increase was also observed in deep structures, including the hippocampus, amygdala and insula. Most of the activations were bilateral, although more extensive in the right hemisphere (Figure 2A; see also Table 1a in Appendix).

With respect to viewing real human body images, BOLD signal increase was mostly found in the same areas that were activated when viewing sculpture images (Figure 2B; see also Table 1b in Appendix). The main difference between the overall activations evoked by the two stimulus-categories laid in the lack of activation of the insular cortex when viewing real human body images (see between-category analysis below).

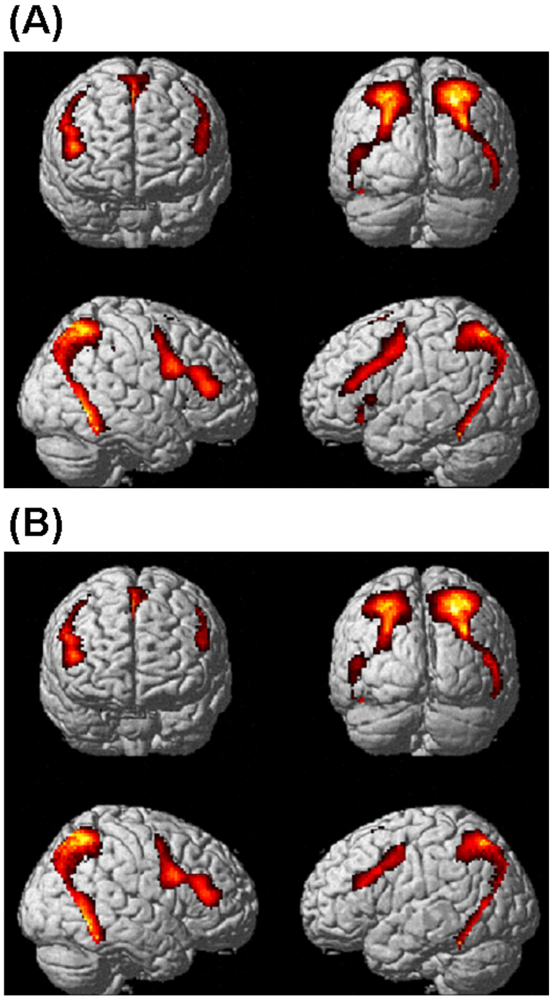

Figure 2. Activations for **(A)** Sculpture and **(B)** real Human Body images versus implicit baseline in *Experiment 1* pulling together canonical and modified stimulus-types across the two experimental conditions (observation and aesthetic judgment). P-FWE corr <0.05.

Between-category differences

Canonical sculpture vs. canonical real human body images

This analysis was carried out comparing activations associated with observation of canonical stimuli only. Direct comparison between sculpture and real human body images across experimental conditions (observation and aesthetic judgment), revealed enhanced activation for canonical sculpture images in the fusiform gyrus bilaterally. Simple contrasts analyses within each experimental condition revealed additional enhanced activation of the antero-dorsal portion of the right insula during aesthetic judgment condition (Figure 3A, B). These results are summarized in Table 2a in Appendix.

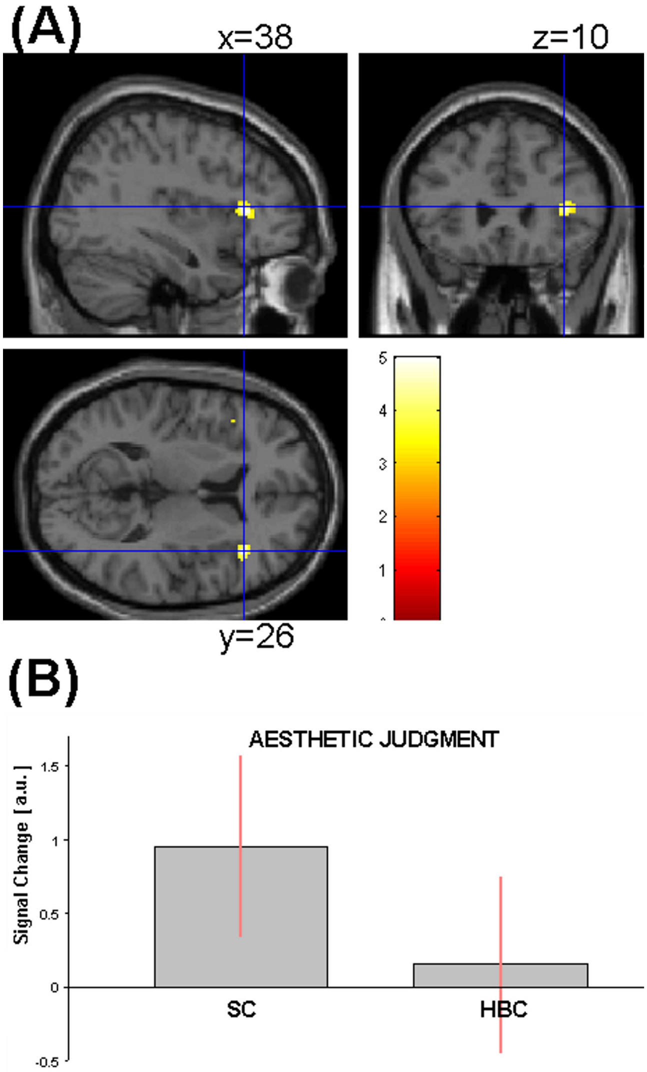

Figure 3. (A) Activation in the contrast canonical Sculpture *minus* canonical real Human Body images (masked incl. by canonical Sculpture images) during aesthetic judgment condition in *Experiment 1*. **(B)** Activity profile within right insula (38 26 10) in arbitrary units (a.u.), +/- 10% confidence intervals (P-FWE corr<0.05).

Canonical real human body vs. canonical sculpture images

Direct comparison between canonical real human body and canonical sculpture images across experimental conditions (observation and aesthetic judgment), revealed enhanced activation for real human body images in right thalamus and in right superior temporal sulcus (STS, 46 -50 10, K_E=63, P-uncorr=0.008). Contrast analysis of simple effects between stimulus-categories for each experimental condition separately revealed that these activations were particularly enhanced during aesthetic judgment condition (Figure 4A, B; see Table 2a in Appendix).

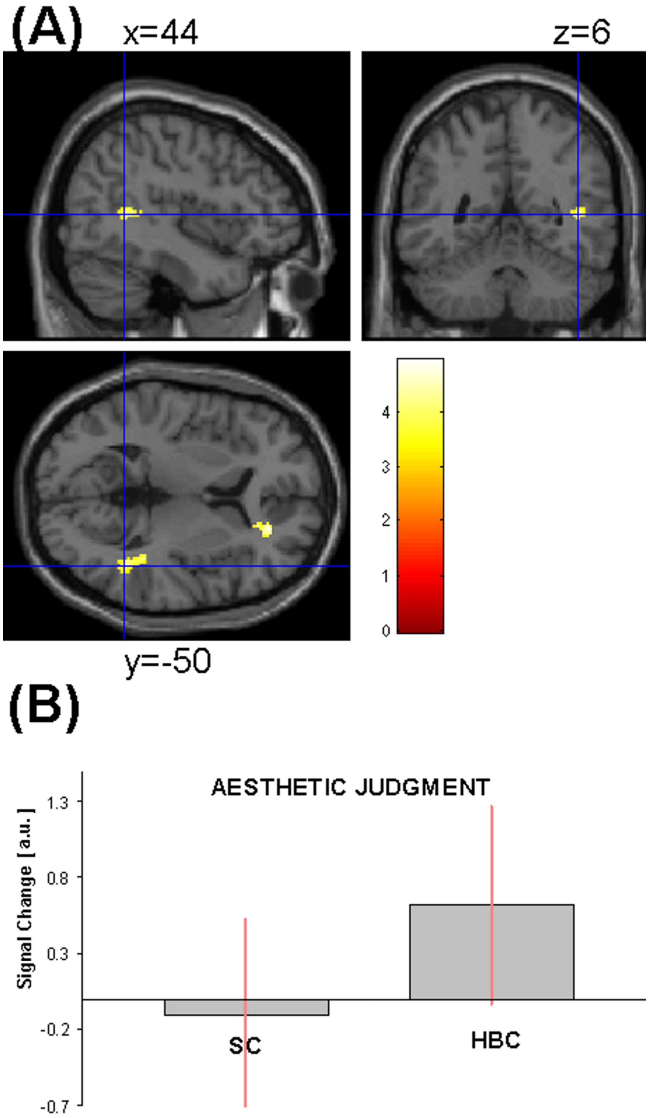

Figure 4. (A) Activation in the contrast canonical real Human Body *minus* canonical Sculpture images (masked incl. by canonical Human Body images) during aesthetic judgment condition in *Experiment 1*. **(B)** Activity profile within right STS (44 -50 6) in arbitrary units (a.u.), +/- 10% confidence intervals (P- uncorr <0.05).

Between-types differences

Canonical vs. modified sculpture images

The direct comparison of canonical *vs*. modified sculpture images produced no significant enhanced activation for either canonical or modified images in neither of the two experimental conditions (observation and aesthetic judgment). These findings are in contrast with the results obtained in our former experiment (Di Dio *et al*., 2007), where the direct contrast of canonical *vs*. modified images across all experimental conditions revealed signal increase for the canonical stimuli in some cortical areas and in right insular cortex, particularly during observation condition (see Experiment 2 below).

Canonical vs. modified real human body images

The direct comparison of canonical minus modified real human body images produced no significant enhanced activation in neither of the two experimental conditions (observation and aesthetic judgment). The opposite direct comparison (modified minus canonical real human body images), on the other hand, produced enhanced activation for the modified images in the left amygdala during observation condition, as well as enhanced activation in a posterior cortical region straddling the inferior and middle temporal gyri during aesthetic judgment condition (see Table 2b in Appendix).

Experiment 2

Overall effect of viewing sculpture and real human body images

In this analysis, we assessed, separately, the overall effect of viewing both *sculpture* (S) and *real human body* (HB) images pooling together brain activations in response to canonical (C) and modified (M) images across the two conditions (observation and aesthetic judgment) with respect to implicit baseline.

Figure 5A shows BOLD signal increase for sculpture images. Most of the activations replicated those observed in Experiment 1 (see Table 3a in Appendix). Activated areas included occipital cortex, fusiform gyrus, lingual gyrus, posterior parietal cortex, inferior parietal lobule, pre-SMA, premotor cortex, and inferior frontal gyrus (IFG). Additionally, enhanced activations were observed in deep structures, including hippocampus, amygdala and the anterior insula. Most of the activations were bilateral. Finally, differently from Experiment 1, signal increase was also found in medial frontal areas, including right anterior cingulate cortex and left orbitofrontal cortex.

Figure 5B shows activations relative to viewing real human body images. Similarly to Experiment 1, BOLD signal increase was found in the same areas that were activated when viewing sculpture images, the major difference being an additional activation at the level of the basal ganglia nuclear complex (see Table 3b in Appendix).

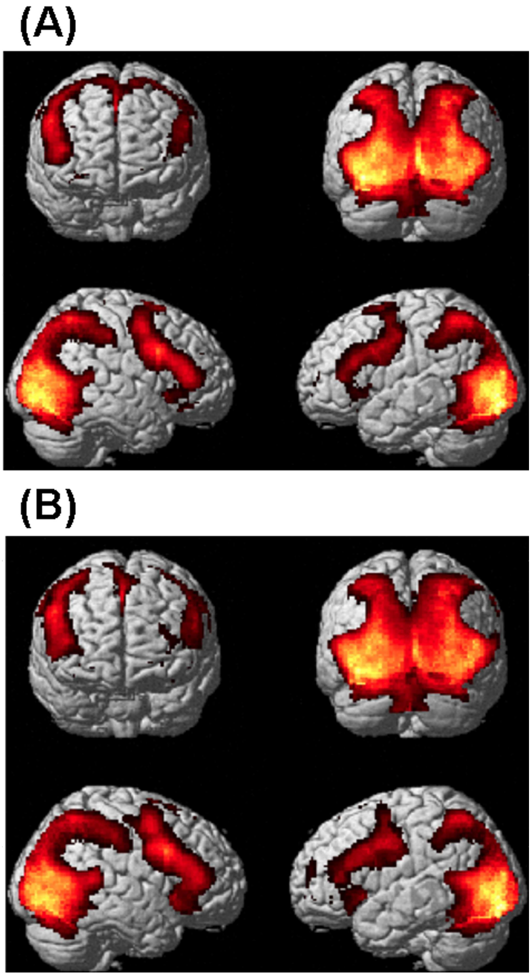

Figure 5. Activations for **(A)** Sculpture and **(B)** real Human Body images versus implicit baseline in *Experiment 2* pulling together canonical and modified stimulus-types across the two experimental conditions (observation and aesthetic judgment). P-FWE corr <0.05.

Between-category differences

Canonical sculpture vs. canonical real human body images

Direct comparison between canonical sculpture and canonical real human body images across experimental conditions (observation and aesthetic judgment) revealed greater activations for sculpture images in lingual and fusiform gyri.

Additional activations were observed from simple contrast analyses. More specifically, during observation condition there was increased activation for canonical sculpture *vs.* canonical human body images in right cuneus, right inferior parietal lobule, right inferior frontal gyrus pars triangularis and pars opercularis, and in the anterior dorsal part of right insula (see Table 4a in Appendix).

Canonical real human body vs. canonical sculpture images

The direct comparison between canonical real human body *vs.* canonical sculpture across experimental conditions (observation and aesthetic judgment) revealed enhanced activations bilaterally in the caudal part of the temporal lobe straddling the middle and superior temporal gyri and extending medially to include the superior temporal sulcus (STS). Simple contrast analyses showed that activation of left STS was particularly strong during aesthetic judgment condition (see Table 4a in Appendix).

Between-type differences

Canonical vs. modified sculpture images

The direct comparison of canonical *vs.* modified sculpture images revealed significant differences during observation condition only. More specifically, signal increase was observed for canonical images in the caudal part of right middle temporal gyrus, inferior frontal gyrus pars triangularis and, crucially, in right anterior dorsal insular cortex (Figure 6A, B; see also Table 4b in Appendix).

The contrast modified *vs*. canonical sculpture images revealed signal increase during aesthetic judgment condition in right supramarginal gyrus and right ventral premotor cortex (BA44) (see Table 4b in Appendix).

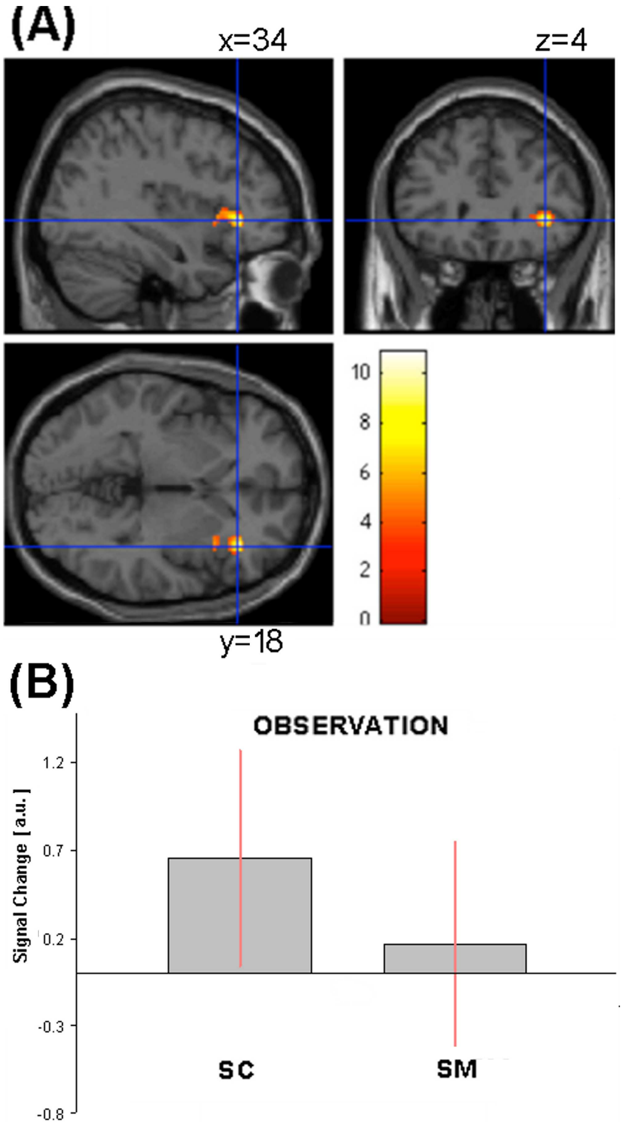

Figure 6. (A) Activation in the contrast Canonical *minus* Modified Sculpture images (masked incl. by Canonical Sculpture images) during observation condition in *Experiment 2*. **(B)** Activity profile within right anterior insula (34 18 4) in arbitrary units (a.u.), +/- 10% confidence intervals (P-FWE corr < 0.05).

Canonical vs. modified human body images

The comparison of canonical *vs*. modified human body images revealed no significant differences. The opposite contrast (modified *vs*. canonical human body images), on the other hand, revealed signal increase for the modified images in ventral premotor cortex (BA44) during observation condition and in superior parietal lobule, inferior temporal gyrus and fusiform gyrus during aesthetic judgment condition. All activations were lateralized in the right hemisphere (see Table 4b in Appendix).

Discussion

In our previous study we showed that activation of the anterior sector of the right insula is associated with the hedonic dimension of aesthetic experience during the observation of artworks. The main purpose of the present study was to investigate whether this specific hedonic response is also present during the observation of non-art biological stimuli. For this purpose, we compared brain activations when participants observed sculpture images with brain activations during the observation of real human bodies represented by photographs of young athletes.

The global pattern of cortical activations during the presentation of sculptures and real human bodies was very similar. Activations included visual occipital and temporal areas, inferior parietal lobule/intraparietal sulcus, ventral premotor cortex and inferior frontal gyrus. Signal increase was also observed in deep structures, such as the hippocampus and amygdala. Most of the activations were bilateral, although more extensive in the right hemisphere. The direct comparison between canonical sculptures and canonical real bodies highlighted, however, some important differences. The observation of sculpture images determined, relative to real human body images, a greater activation of *right anterior dorsal insula,* as well as activation of some visual areas and, in particular, of fusiform gyrus. The opposite contrast (human body minus sculpture images) showed a greater activation of the superior temporal sulcus (STS).

It is known from both monkey (see Desimone et al., 1984; Tsao et al., 2006; Gross, 2008) and human studies that portions of the inferotemporal lobe and of its human homologue (the fusiform gyrus), play a crucial role in the processing of faces (for review see McKone and Kanwisher, 2005;

Gross, 2008). Furthermore, it was also shown that some sectors of fusiform gyrus encode, with nearly the same level of selectivity, images of human bodies (Peeling and Downing, 2004; Schwarzlose et al., 2005). In this light, it is plausible that the fusiform activation observed in the present study reflected a detailed visual analysis of the physical aspects of the body (e.g. size, shape, proportion) of the sculpture as compared to real human images.

The comparison between real human body vs. sculpture images showed a consistent activation of the superior temporal sulcus (STS). STS is a region known to be involved in visual processing of movement of body parts. Thus, STS activation was likely due to a matching between the observed human body images and the representation of body movement encoded in this region (see Perrett et al., 1989; Allison et al., 2000; Thompson et al., 2005; Pelphrey et al., 2004). Note that, although in the present study we used static stimuli, there is evidence that these stimuli, when implying motion, are able to activate visual areas encoding overt movements, as shown for area MT/V5 by Kourtzi and Kanwisher (2000).

In the present study, both sculpture and real body images contained an even number of static and dynamic stimuli. It is then likely that activation differences observed between real body and sculpture images were not be ascribed to differences in some stimulus properties (such as dynamism), but rather to different attention deployment in the two cases. Attention was more focused on action in the case of real human images, whilst it was more focused on the physical aspects of the body in the case of sculpture images. In turn, these different attention allocations could be related to different attitudes towards the presented images. In the case of the real human body, the implicit attitude of the observers would be that of trying to understand the meaning of the represented gestures and, possibly, the intention of the observed individuals. In contrast, the sculptures constitute an artistic representation of the human body and the spontaneous attitude of the observers would be that of exploring them with the purpose of appreciating their physical properties.

The most important finding of our study lays, however, in the activation of right insula in the contrast sculpture vs. real human body images. The activated part of the insula was located in its rostro-dorsal sector. This sector corresponds to the insular region also found activated in our previous study in the contrast canonical vs. modified sculpture images (Study 1) and confirmed from the same contrast in Experiment 2 of the present study. Since canonical proportions are positively related to aesthetic evaluation of sculpture images, we interpreted this activation as the hedonic signature of aesthetic experience when viewing artworks.

Insula is an extremely complex and heterogeneous structure including a posterior granular (sensory part), a central large dysgranular and a small rostro-ventral agranular (motor and vegetative parts) sector (see Mesulam et al., 1982, 1985; Augustine, 1996). A recent meta-analysis of the human insula by Kurth et al. (2010) revealed four functional distinct regions corresponding to sensory-motor, olfacto-gustatory, social-emotional and cognitive networks of the brain. Social-emotional aspects activate the ventro-rostral part of the insula while all tested functions, except for sensory-motor function, overlap on its anterior dorsal portion. These data allow one to specify better the functional role of this region in mediating hedonic experiences when viewing artworks. This region is not encoding the mere emotional aspect of the stimuli, but integrates cognitive and emotional processes to create a coherent experience of the attended stimuli. Although activation of this region is not uniquely deputed to aesthetic experience (see Kurth et al., 2010), our results indicate that it plays a fundamental role in providing an hedonic quality to art processing.

One may argue that insular activation observed for sculpture images, and not for real human body stimuli, could have been triggered by the sculptures complete nudity, a factor that was not counterbalanced between categories. In this respect, some experimental evidence coming from studies investigating the neural correlates of emotional response to arousing stimuli report insula activation. Often, the arousing stimuli represent film clips or photographs depicting nudes and sex scenes (e.g., Stoleru et al., 1999; Gizewski et al., 2006; Safron et al., 2007). In these studies, right ventral insula and/or left insula were found activated when attending arousing stimuli. The rostro-ventral insular sector found activated in these studies is different from the more dorsal sector observed in our study. Anterior ventral insula is often associated with a representation of autonomic states (e.g., Critchley et al., 2002) and with the presentation of stimuli holding a socio-emotional status (see Kurth et al., 2010 for a review). Most noteworthy, our results indicate that the insular sector found activated in the contrast sculpture *vs.* real human body stimuli showed also a lower activation in association with decreased aesthetic valence conveyed by the proportion-modified stimuli. For this reason, we suggest that the right antero-dorsal insular activation observed for sculpture images in the present study is evoked by an hedonic state associated with the aesthetic dimension of the sculptures and not with their nudity.

Insular activation was absent in the case of observation of real human body images, irrespective of proportion modification. It is worth noting, in this respect, that behavioural data showed that proportion affected aesthetic rating in both stimulus-categories; namely, the canonical images were preferred to modified images also in the case of real human bodies. What these data seem to suggest is that the enhanced insular activation observed for sculpture images compared to real body images, and particularly for canonical ones, emerged from attendance to specific physical properties of the sculpture images that, when altered, determined a diminished hedonic response in the viewer. This specific hedonic response was not present when judging the aesthetics of real body images. This does not imply that there is no aesthetic experience associated with the viewing of real body images. However, our data show that this experience does not have the same neural substrates as those underpinning the viewing of sculptures. Exploration of the neural correlates associated with aesthetic experience for real human bodies was beyond the purpose of the present study and we cannot assert any conclusions on this issue.

Concluding considerations

Here we tested whether the neural activations underpinning hedonic experience when viewing an artistic representation of the human body (masterpieces of Classical art) are also present when observing images of non-art biological stimuli (real human bodies). Imaging results indicated that aesthetic experience for artworks recruited the anterior sector of right dorsal insula. This sector was not activated when attending real human body images suggesting that the hedonic value underpinning the aesthetic appraisal of artworks has a character of it own, distinct from that characterizing the aesthetic appraisal of non-art material.

2.2 Behavioural and Eye-Tracking Studies

2.2.1 Study 3 - The body in art: A comparative study of aesthetic evaluation between sculpture and real-human-body images

Artworks are typically intentionally designed by an artist to express a meaning (Kapoula et al., 2010). This meaning may be formally conveyed through the use of specific structural strategies so to, for example, affect the perceptual weights of the most significant elements (Nodine, 1982; Locher, 1996). The human form is unique in its genre since, through its structural properties, may convey meanings that have behavioural and social salience, possibly impelled by biological drives.

The attraction power of the human form was already shown in one of the very first attempts to investigate perception in art in the early thirties. Using an eye tracking technique, Bushwell (1935) presented participants with images of different artworks and observed that, although the global scanning path was quite heterogeneous among participants, there was a general tendency to scan the paintings using global and local strategies and, importantly, to concentrate on high-contrast regions. These regions included faces and human forms.

Of great interest has often been, in the study of the human form, the face region, which has been shown to be a strong catalyst of attention. In Tatler et al. (2007), for example, subjects performed smaller saccades when viewing geometrical patterns with an embedded face than when viewing the geometrical forms alone. Smaller saccades were interpreted by the authors as indexing greater attraction to the face.

The aesthetic value of a face may be strongly associated with its structural outline, as suggested in studies showing the effect of symmetry on face attractiveness (e.g. Mealey et al., 1999; Penton-Voak et al., 2001; Little & Jones, 2003; 2006). In their study, Little & Jones (2003), for instance, contrasted two different accounts for symmetry preference: the evolutionary advantage account and the perceptual bias account, based on the perceptual facilitation explanation for symmetry preference. Their results favoured the evolutionary advantage account, suggesting a biological basis for symmetry preference, as also shown by cross-cultural agreement on the attractiveness of symmetry (Rhodes et al., 2001b).

A strong perceptual force within an image is also exerted by the human body. In art, the distinctiveness of the human form in perceptual terms is highlighted in studies showing, for example, that contextual and semantic factors play an important role in preference given to artworks with poor semantic values, such as landscapes and abstract works, and to representational works with high semantic values. These latter are prominently constituted by portrays (Graham et al., 2010).

In contrast to the face region, little attention has been devoted to the attractive power of the body and to the aesthetic constituents associated with its attractiveness. Some studies (Di Dio et al., 2007; 2011) have shown that, in Classical art, the aesthetics of the human body is strongly related to its structural makeup that, in these masterpieces, highly reflects the structural properties of the real body. Art, on average, possesses the same correlation structure as natural objects (for a review, see Simoncelli & Olshausen, 2001), which are shown to share fractal-like, scale-invariant statistical properties (Redies et al., 2007). The human aesthetic sense may be then based on general principles of perception that have been important during evolution of biological signals (Enquist & Arak, 1994).

On this basis, it was then interesting to evaluate whether similar content depictions, belonging to different categories (art and non-art), are aesthetically evaluated according to the same principles or whether categorical differences lead to different perceptual and behavioural responses. This topic was explored in the present study by investigating aesthetic responses to the human body, which carries a strong biological inherent meaning. The aesthetic evaluation of the human body was investigated presenting subjects, naïve to art criticism, with images representing Classical sculpture images (art category) and images of real human bodies (biological non-art category). Aesthetic judgment was assessed as a function of body proportion, which was shown to be strongly associated with the aesthetic character of Classical sculptures. In Di Dio et al. (2007; 2011), in fact, a controlled manipulation of the proportion between body parts determined a systematic decrease in the aesthetic evaluation of the presented stimuli. Considering that other parameters could be associated with the beauty of these Masterpieces, it is important to note that proportion manipulation was not aimed at testing the effect of proportion *per se*. Rather, it represented an experimental opportunity to assess aesthetic variations as a function of a quantifiable variable. On this basis, in the present study we carried out specific modifications of the body-proportion in both stimulus categories (art, biological non art; see Figure 1 for an example of the stimuli).

The perceptual component associated with the aesthetic evaluation of the stimuli was studied using the eye-tracking technique. Studies investigating attention suggest that eye movements index overt selection and, as a consequence, they are the expression of the relation between what is observed and its relevance to the viewer's interest (Rizzolatti et al., 1987; Palmer, 1999). In line with this general idea, various studies investigated the first stages of aesthetic experience of visual artworks by exploring eye-movement behaviour (Locher, 1996; 2006). Some eye tracking measures, such as fixation density, have indeed been shown to index the observers' interest in informative elements of the image (see Nodine et al., 1993; Henderson & Hollingworth, 1999).

In the present study, analysis of behavioural and eye tracking data was aimed at elucidating whether possible differences in aesthetic evaluations between the two stimulus-categories could be attributed to perceptual differences in identifying proportion and/or to attendance to some category-specific salient aspects.

To maintain structural similarities across stimulus-categories, all stimuli depicted male bodies. To explore whether cross-gender attractiveness (i.e., female subjects observing male figures) is affected by stimulus category (art *vs*. biological non-art) or whether similarities within-gender (i.e., males viewing male bodies) biased aesthetic judgment towards one specific stimulus-category, psychophysical responses were also analyzed as a function of gender.

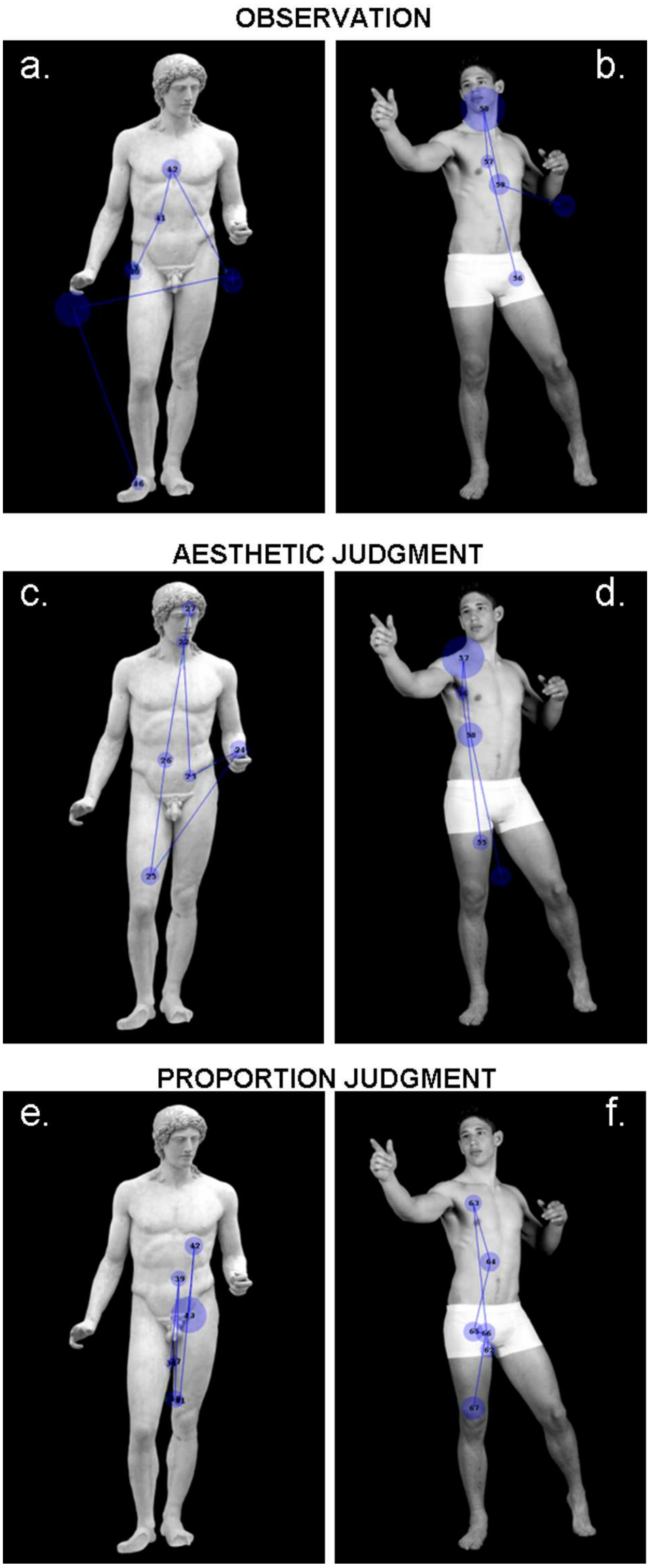

Figure 1. Example of stimuli used in this study with a superimposed track of eye movements. The lines indicate the looking pattern of one single participant, whereas the blobs indicate the areas attended the most averaged across all participants. The dimension of the blobs depicts the fixation time (ms) at each location. The top images (**a.**, **b.**) show the participant's eye gaze behaviour during observation task; the middle images (**c.**, **d.**) during aesthetic judgment task; the images at the bottom (**e.**, **f.**) during proportion discrimination task.

Experimental Procedure

Participants

Twenty-two healthy volunteers participated in this study (11 males, 11 females; mean age 24 years). The subjects were undergraduate and graduate university students, naïve to art criticism. All of them had normal or corrected to normal vision. All subjects gave their informed consent to participate in the study, which was approved by the Local Ethics Committee (Parma).

Stimuli

In order to investigate differences in aesthetic evaluation of art *vs*. non-art stimuli, the subjects were presented with images of Classical sculptures (S – art category) and images of real human bodies (HB – biological non-art category).

Original sculpture images were selected from Classical examples that met the golden ratio criteria (proportion torso: legs (T-L)=0.62±0.01 – canonical S stimuli). The selected HB images also met the golden ratio criteria (proportion torso: legs (T-L)=0.62±0.02 – canonical HB stimuli). Each of the 28 sculpture images represented a different sculpture. The 28 HB images represented 8 different athletes that were purposely photographed for this experiment by a professional photographer. The athletes posed following specific poses shown by an actor according to the body postures depicted in the sculpture images. Of all HB photographs taken, pictures were selected, which best matched the poses expressed by the sculptures. Accordingly, 4 different poses were selected for 5 different athletes, 3 poses for 2 athletes, and 2 poses for 1 athlete. All images were black and white and represented only male bodies that were comparable across categories in terms of body structure and proportion.

A new set of stimuli was created from the original/canonical one for both S and HB by altering the torso:legs (T-L) ratio of the canonical images. These new 2 sets of stimuli were thus identical to the canonical ones (in terms of factors such as content, viewing perspective, Colour and luminescence) except for proportion. Within the modified stimuli, we created two modification types: one type of modification (M1) was made with short torso and long legs (modification range T-L=0.5–0.6), whereas the second type of modification (M2) was created with long torso and short legs (modification range T-L=0.64-0.75). Within both M1 and M2 modification-types, the stimuli differed in the extent of their modification. More specifically, the T-L relation was modified for each category as follows: 6 M1 and 6 M2 stimuli underwent a small-modification extent (0.57–0.59; 0.64–0.66), 4 M1 and 4 M2 stimuli a medium-modification extent (0.54-0.56; 0.67-0.72) and 4 M1 and 4 M2 stimuli underwent a high-modification extent (0.51-0.53; 0.73-0.75). In total 56 images of sculptures (28 canonical and 28 modified) and 56 HB images (28 canonical, 28 modified) were created for the experiment.

Procedure

During the experiment, the subjects sat in a quiet and dimly lit room. The stimuli were presented on a laptop screen in three different tasks: observation (O), aesthetic judgment (AJ) and proportion discrimination (PD). During tasks performance, the subjects' eye movements were recorded using the eye-tracking technique (see Apparatus section). Eye-gazing behaviour was recorded within each task, so to highlight possible distinctive gazing patterns associated with each task as a function of stimulus categories and types. For this purpose, 5 independent areas of interest (AOIs) were created within each single image. The AOIs corresponded to the Face area (including the face and neck areas), the Left Hand area (including left arm and hand), the Right Hand area (including right arm and hand), the Torso area (extending from the base of the neck down to the pelvis) and the Leg area (including the pelvis and both legs). Fixation duration (ms) was taken as dependent measure within each AOI.

Subjects were blind to the aim of the experiment to not affect their spontaneous response to the stimuli, particularly during observation task. The experimental tasks were explained in details step by step throughout the experimental sessions. The general instructions provided at the beginning of the experiment informed the subjects that they would have seen images representing sculptures and images of young athletes. Subjects were required to relax and explore the content of the image in full.

The subjects carried out the observation task first, followed by the aesthetic judgment task and proportion discrimination last. The task order was maintained fixed for all subjects to not affect their attitude towards the observed images with previous instructions. More specifically, during observation task, we wanted to capture the most spontaneous, cognitively unbiased, response to the stimuli. Presenting either aesthetic or proportion tasks first would have biased the observation task accordingly. Similarly, presenting PD before AJ could have possibly affected the subsequent aesthetic rating of the images as a function of the overt recognition of the stimuli proportion/disproportion.

During aesthetic judgment task, the subjects had to rate the stimuli on a scale from 0 (very ugly) to 7 (very beautiful) by pressing the corresponding bottom on a computer keyboard. By using a continuous scale, we aimed at increasing sensitivity to the aesthetic assessment of the stimuli. To evaluate the subject's ability to discriminate the stimuli as a function of our manipulation of the body proportion, during proportion discrimination task, the subjects had to rate the proportion of the stimuli on a dichotomous measure (0 – disproportioned; 1 – proportioned).

Each task was carried out in separate sessions. The whole experiment was therefore composed of 3 sessions. Each task/session was characterized by the presentation of 7 blocks of sculpture and 7 blocks of HB images. Each block contained 8 stimuli pertaining to the same category (art and non art); the stimuli were presented, in a randomized order, for 2000 ms once for each task. The blocks were randomized within each session and across subjects.

Apparatus

A corneal reflection technique (Tobii x 50, Tobii Technology AB) was used to record the subjects' eye-gaze direction on the basis of reflection of the near infrared light on the cornea and pupil. Subjects sat at a distance of 70 cm from the computer (Acer) screen. The eye-tracker was positioned at 40 cm from the laptop screen. Since we had to deliver appropriate instructions to the subjects prior each task, calibration was made for each subject at the beginning of each experimental session with the program Clearview2.7.1. The same software was used for stimuli presentation and behavioural data collection. Eye-movement data were continuously sampled at 50 Hz, processed offline using Clearview Excel templates and then exported to SPSS16.0 for statistical analysis.

Results

The results are divided into behavioural responses recorded during aesthetic and proportion discrimination tasks and eye-gazing behaviour produced in all 3 experimental tasks (observation, aesthetic judgment, proportion discrimination). The results are presented in separate sections. Results for the aesthetic judgments are presented first followed by the results for the proportion discrimination task. Results for the eye-tracking data are presented last.

Behavioural Results - Aesthetic Judgment

In this analysis, we compared the behavioural scores obtained for male and female subjects during aesthetic judgment task in response to the canonical and modified images for the two stimulus-categories (S, HB). Table 1a (see Appendix) shows a summary of the obtained results and statistics. Data analyses were carried out using repeated measures general linear models (GLM) and Greenhouse-Geisser values are reported when the sphericity assumption was violated (Mauchly's

Test of Sphericity, $p<0.05$). Bonferroni correction was employed for all post-hoc multiple comparisons.

Canonical vs. Modified: effect of modification degree

Within this analysis, we compared aesthetic judgment ratings obtained for the canonical sculpture (SC) and canonical HB images (HBC) with their corresponding modified versions, using gender as between groups factor. The modified versions were created with 3 modification degrees (small, medium and high – see Stimuli section). Accordingly, a repeated measures 2x4x2 analysis with 2 levels of image category (S, HB) and 4 levels of modification degree (canonical -no modification-, small, medium, high) as within subjects factors and gender as a between subjects factor was carried out in order to measure the effect of image proportion on aesthetic judgment.

Results showed a main effect of stimulus-category (S>HB; $F_{1,20}=14.49$, $p=.001$, partial-$\eta^2=.42$, $\delta=0.95$; see Figure 2a), a main effect of modification degree ($F_{3,60}=13.9$, $p<.001$, partial-$\eta^2=.38$, $\delta=1$) and a significant modification-degree*gender interaction ($F_{3,60}=13.9$, $p<.037$, partial-$\eta^2=.13$, $\delta=.68$; see Figure 2b). Tests of within subjects effect showed that, independently of stimulus category (S, HB), subjects rated canonical images as the most beautiful and high-modification degree images as the least beautiful, with significant differences in aesthetic rating between every modification level (C>Msmall; $F_{1,20}=6.3$, $p=.02$, partial-$\eta^2=.24$, $\delta=.66$), (Msmall>Mmedium; $F_{1,20}=13.6$, $p=.001$, partial-$\eta^2=.4$, $\delta=.94$), (Mmedium>Mhigh; $F_{1,20}=11.2$, $p=.003$, partial-$\eta^2=.36$, $\delta=.89$).

With respect to the interaction modification-degree*gender, tests of within-subjects contrast revealed that the source of interaction had to be searched within the difference in aesthetic judgment between canonical and small-modification degree images ($F_{1,20}=4.8$, $p<.04$, partial-$\eta^2=.19$, $\delta=.54$).

Post-hoc comparisons were carried out to investigate the sources of these differences within gender. Results showed that the difference in aesthetic rating between canonical and small-modification degree stimuli was observed for female subjects only ($F_{1,10}$=8.6, p<.015, partial-η^2=.62, δ=.75).

Canonical vs. Modified: effect of modification type

Within this repeated measures 2X3X2 analysis, we compared aesthetic judgment ratings for the canonical sculpture and HB images with their corresponding modified versions (C – no modification -, M1, M2), using gender as between groups factor (see Figure 2c).

Results revealed a main effect of stimulus-category (S>HB; $F_{1,20}$=9.73, p=.005, partial-η^2=.33, δ=.84), a main effect of stimulus-type ($F_{2,40}$=26.7, p<.001, partial-η^2=.57, δ=.1), a significant interaction stim-type* gender ($F_{2,40}$=6.9, p=.003, partial-η^2=.26, δ=.90), and a significant 3-way interaction stim-cat* stim-type*gender ($F_{2,40}$=4.8, p=.013, partial-η^2=.2, δ=.77).

Differences of within-subjects contrasts testing for simple effects revealed a significant difference in aesthetic judgment between C and M1 stimulus-types (C>M1; $F_{1,20}$=5.8, p=.026, partial-η^2=.23, δ=.63), between C and M2 (C>M2; $F_{1,20}$=34.5, p<.001, partial-η^2=.63, δ=1), as well as between M1 and M2 modification-types (M1>M2; $F_{1,20}$=43.2, p<.001, partial-η^2=.68, δ=1). Additionally, simple contrast analysis testing for the 2-way stimulus-type*gender interaction effect revealed a significant gender interaction between canonical and both modified stimulus-types images (C>M1: $F_{1,20}$=6.2, p=.021, partial-η^2=.24, δ=.66; C>M2: $F_{1,20}$=9.02, p=.007, partial-η^2=.31, δ=.82)

Post-hoc comparisons testing for stimulus-type*gender interaction compared aesthetic ratings observed for canonical stimuli with those ascribed to M1 and M2 modification-types, across stimulus category (S, HB), independently for each gender group. Results revealed a significant difference in aesthetic rating between C and M1 only for the female subjects ($F_{1,10}$=7.1, p=.024, partial-η^2=.41, δ=.99), as well as a significant difference between C and M2 stimulus-types in both gender categories (females: $F_{1,10}$=24.99, p=.011 partial-η^2=.71, δ=.99; males: $F_{1,10}$=9.7, p=.011 partial-η^2=.42, δ=.80).

Finally, simple contrast analysis testing for the 3-way stim-cat*stim-type*gender interaction effect revealed that the source of interaction was to be searched within the difference in aesthetic ratings between M1 and M2 modification-types ($F_{1,20}$=7.9, p=.011 partial-η^2=.28, δ=.76). Accordingly, we carried out a 2x2 repeated measures analysis within each gender group with two levels of stimulus-category (S, HB) and 2 levels of stimulus-type (M1, M2). With respect to female subjects, results revealed a main effect of stimulus-type (M1>M2, $F_{1,10}$=24.4, p=.001, partial-η^2=.71, δ=.99) and a stimulus-category*stimulus-type interaction ($F_{1,10}$=5.8, p=.037, partial-η^2=.37, δ=.58). Post-hoc comparisons testing for the interaction effect revealed a significant difference in aesthetic rating for female subjects between M1 and M2 stimulus-types for the sculpture images only (M1>M2, $F_{1,10}$=10.95, p=.008, partial-η^2=.52, δ=.85). As far as male subjects are concerned, the 2x2 GLM analysis revealed a main effect of stimulus-category (S>HB, $F_{1,10}$=8.13, p=.017, partial-η^2=.45, δ=.73) as well as a main effect stimulus-type (M1>M2, $F_{1,10}$=13.3, p=.004, partial-η^2=.57, δ=.91).

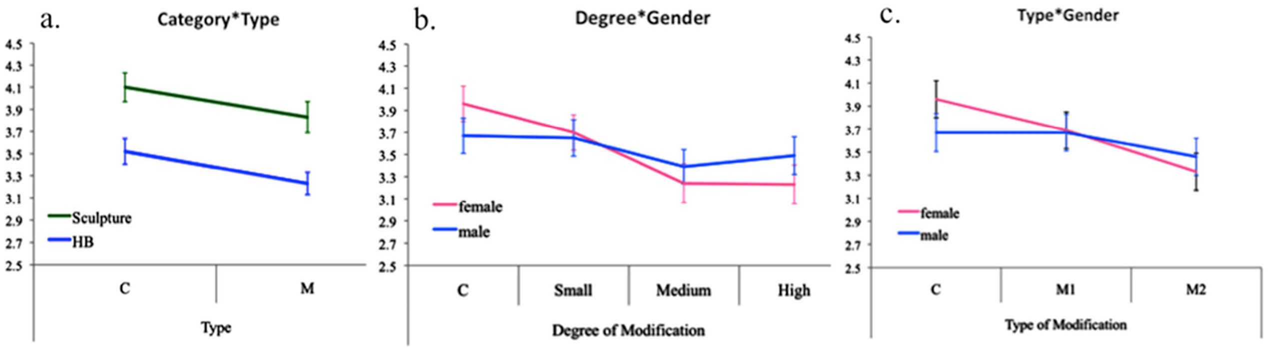

Figure 2. Mean scores during aesthetic judgment task for **a.** canonical (C) and modified (M) sculpture (S - green line) and real human body images (HB - blue line). **b.** Effect of modification degree (canonical, small, medium and high) on mean aesthetic judgment scores as a function of gender across stimulus category (S, HB). **c.** Effect of modification type (modified M1, modified M2) on mean aesthetic judgment scores as a function of gender across stimulus category (S, HB). Error bars represent the standard error of the means.

Behavioural Results - Proportion Discrimination task

Proportion rating was taken on a dichotomous measure (0=disproportioned; 1=proportioned). Data were analyzed as a function of visual discrimination using d-prime scores. The d-prime analysis is a test of measurement sensitivity based on the standardized difference between proportion of false alarms (modification present: no, modification detected: yes) and proportion of correct responses / hits (modification present: yes, modification detected: yes).

Using this method, we calculated d-prime scores as a function of *false alarms*, represented by incorrectly identified modified images within the canonical stimuli, relative to *hits*, represented by the modified images correctly identified within the modified stimuli, in both stimulus categories (S, HB). Accordingly, 3 new indexes of visual discrimination were calculated with respect to small, medium and high modification-degrees, and 2 new indexes with respect to modification-types (M1, M2). Since each canonical stimulus underwent a specific modification, canonical stimuli were used in association with their respective modification. Thus, for example, d-score for small modification-degree in M1 modification-type were calculated from the relative modified set (M1small) and from the canonical set they originated from (C_M1small).

These new indexes were then used in two independent repeated measures ANOVAs (stimulus-category, modification-degree/stimulus-type, gender) to evaluate the subjects' ability to detect proportion modification of sculptures and HB. Indexes approximating 0 indicated poor discrimination. The more negative the indexes, the more accurate the identification of the modified stimuli within the relative modified stimulus-sets.

The main results for PD task are summarized in Table 1b (see Appendix).

Canonical vs. Modified: effect of modification degree

Within this 2x3x2 repeated measures analysis, we compared d-prime scores reflecting accuracy in proportion identification for the modified sculpture and HB images (stimulus-category) as a function of modification-degree (small, medium and high), using gender as between groups factor.

Results showed a main effect of modification-degree only ($F_{2,40}$=5.4, p=.009, partial-η^2=.21, δ=0.81). Tests of within subjects effect contrasts showed that, independently of stimulus category (S, HB) and gender, subjects discriminated more accurately modified images with high level of modification compared to images with medium level of modification (Mhigh>Mmedium; $F_{1,20}$=4.8, p=.04, partial-η^2=.2, δ=.55), and images with medium level of modification as compared to images with small modification-degree (Mmedium>Msmall; $F_{1,20}$=10.6, p=.004, partial-η^2=.35, δ=.87).

Canonical vs. Modified: effect of modification type

Within this 2x2x2 repeated measures analysis, we compared d-prime scores reflecting accuracy in proportion identification for the modified sculpture and HB images (stimulus-category) as a function of modification-type (M1, M2), using gender as between groups factor.

Results showed an interaction effect between category (S, HB) and stimulus-type (M1, M2; $F_{1,20}$=5.6, p=.029, partial-η^2=.22, δ=.61), as well as a significant 3-way category*type*gender interaction ($F_{1,20}$=7.39, p=.013, partial-η^2=.27, δ=.74). Post-hoc comparisons testing for category*type interaction, independently of gender, showed that M1 modification-type was detected less accurately compared to M2 modification-type for sculpture images ($F_{1,21}$=6, p=.023, partial-η^2=.22, δ=.65) and that M2 modified sculpture images were detected more accurately than M2 modified HB images ($F_{1,21}$=5.1, p=.035, partial-η^2=.19, δ=.58).

The 3-way interaction was explored examining the relation between discrimination accuracy for stimulus-category and type within each gender group. Accordingly, two separate 2x2 repeated measures analyses were carried out within each group, with two levels of stimulus-category (S, HB) and two level of stimulus-type (M1, M2). With respect to the male subjects, no significant differences were observed, as indexed by the lack of significant main and interaction effects ($p>.05$). With respect to the female subjects, results revealed a significant category*type interaction ($F_{1,10}=14.16$, $p=.004$, partial-$\eta^2=.59$, $\delta=.92$). Post-hoc comparisons revealed no significant differences between stimulus-types within and between categories. However, effect size indexes associated with each comparison revealed that most of the variance in discrimination accuracy originated from the difference between M1 and M2 stimulus-types within the sculpture category (SM2>SM1: $F_{1,10}=4.25$, $p=.067$, partial-$\eta^2=.30$, $\delta=.46$) as well as from greater accuracy in detecting M2 stimulus-type in the sculpture compared to HB category (SM2>HBM2: $F_{1,10}=4.17$, $p=.068$, partial-$\eta^2=.29$, $\delta=.46$). Failure to reach significance in these contrasts could be possibly due to the small sample size, as suggested by low power indexes.

Eye-gazing Results

Statistical analysis of the data was carried out for the *canonical* and *modified* sculpture and HB images for each experimental task separately. Due to the lack of data in more than half of trials, 5 subjects were excluded from the data analysis in aesthetic judgment and proportion discrimination tasks and 6 participants were excluded from data analysis in observation task.

The areas of interest (AOIs) were defined independently for each image and corresponded to the Face, Left Arm, Right Arm, Torso and Leg areas (see *Procedure* section for details).

Statistical analysis was carried out using the average fixation duration (ms) at any particular area of interest. Since each AOI was of a different dimension (e.g., the Face area being about 5 times smaller than the Leg area), fixation duration within each AOI was corrected to the size of the areas occupied in the image. The weight (q) of each AOI was therefore calculated as a relation of mean AOI size to 1/5 of the sum of all AOIs. For example, the Face area occupied 10% of the whole image, therefore the time exposure to the Face area was multiplied by q=(100%/5)/10%.

A repeated measures 2x2x5x2 factorial analysis (GLM) with 2 levels of image category (S, HB), 2 levels of image-type (C, M), and 5 levels of Areas of Interest (Face, Left Arm, Right Arm, Torso and Leg area) as within subjects factors and gender as between subjects factor was carried out separately for observation, AJ and PD tasks. Post-hoc comparisons were carried out to further explore main effects and interaction effects using Bonferroni *p*-corrected values for all multiple comparisons.

A representative example of eye gazing behaviour is shown in Figure 1.

Observation task

A repeated measures 2x2x5 factorial analysis revealed a main effect of Category (HB>S, MD=46 ms, S.E.=9.78, $F_{1,15}$=25.3 $p<.001$, partial-η^2=.64, δ=.99), a main effect of AOI ($F_{2,60}$=9.66, p=.001, partial-η^2=.41, δ=.97) as well as a significant 3-way interaction Category*Type*AOI ($F_{2,60}$=4.59, p=.019, partial-η^2=.26, δ=.73). No gender differences in fixation duration were found for observation task.

With respect to the main effect of AOI, post-hoc comparisons showed that, independently of stimulus type and category, participants fixated longer on the Torso area compared to all other areas (Torso>Face: MD=46 ms, S.E.=9.78, $p<.001$; Torso>Left Arm: MD= 457 ms, S.E.=56.21, $p<.001$; Torso>Right Arm: MD=463 ms, S.E.=55.8; $p<.001$; Torso> Leg.: 375 ms, S.E.=49, $p<.001$).

Additionally, post-hoc comparisons testing the 3-way interaction stimulus-type*category*AOI revealed that the subjects attended longer to the Face and Torso areas of HB images compared to sculpture images for both canonical (Face: MD=152 ms, S.E.=41, p=.002, Torso: MD=70 ms, S.E.=11.8, p<.001) and modified stimulus-types (Face: MD=48 ms, S.E.=17.5, p=.02; Torso: MD=75 ms, S.E.=14.5, p<.001).

Aesthetic judgment task

A repeated measures 2x2x5x2 analysis revealed a main effect of Category (HB>S, MD=108 ms, S.E.=35, $F_{1,15}$=9.6, p=.007, partial-η^2=.39, δ=.93), a main effect of AOI ($F_{2,60}$=13.05, p<.001, partial-η^2=.47, δ=.99), a significant interaction AOI*stimulus-category ($F_{2,60}$=4.59, p=.019, partial-η^2=.26, δ=.73), a significant interaction AOI*stimulus-type ($F_{2,60}$=3.5, p=.004, partial-η^2=.19, δ=.84) as well as 3-way Category*type*AOI interaction ($F_{2,60}$=5.4, p=.01, partial-η^2=.27, δ=.81). No gender differences in fixation duration were found.

Post-hoc comparisons were carried out to explore the main and interaction effects between category, stimulus-type and fixation duration at any particular area of interest. Exploring the main effect of AOI, independently of stimulus category and type, results showed that the most attended areas were the Torso, followed by the Face area. Fixation duration between these two areas was not significantly different (p>.05). In contrast, significant differences were observed between the Torso and all other areas in the following order: Torso>Left Arm (MD=209 ms, S.E=43, p=.02); Torso>Right Arm (MD=315 ms, S.E.=55, p<.001); and Torso>Legs (MD=372 ms, S.E.=55, p<.001). Finally, besides the Torso and the Face areas, the most attended area was the Left Arm, which was fixated significantly longer than both the Right Arm (MD=106 ms, S.E.=18.5, p<.001), and the Leg area (MD=163 ms, S.E.=30, p=.001).

Post-hoc comparisons analysing the interaction effect between AOI and stimulus-category showed that, independently of stimulus type, participants fixated significantly longer on the Face and the Left Arm areas of HB images compared to sculpture images (MD=227ms, S.E.=99, *p*=.036; MD=274ms, S.E.=48, *p*<.001).

Post-hoc comparisons testing the interaction effect between AOI and stimulus-type further indicated that, independently of stimulus-category, participants fixated longer on the Torso and the Left Arm areas of the canonical images than the Left Arm and Torso areas of their modified counterparts (MD=123 ms, S.E.=49, *p*=.02; MD=125 ms, S.E.=57, *p*=.05, respectively).

Finally, the 3-way interaction between stimulus-category, stimulus-type and AOI showed that participants fixated longer on the Face and Left Arm areas when presented with canonical HB images compared to canonical sculpture images (Face: MD= 160 ms, S.E.=63, *p*=.02; Left Hand: MD= 432ms, SE=83, *p*<0.001).

Proportion discrimination task

A repeated measures 2x2x5x2 analysis showed a main effect of Category (HB>S, MD=46 ms, S.E.=9.8, $F_{1,15}$=22.6, *p*<.001, partial-η^2=.6, δ=.99), a main effect of AOI ($F_{2,60}$=41, *p*<.001, partial-η^2=.73, δ=1), and no effect of stimulus-type (*p*>.05). No gender differences in fixation duration were found for PD task

Post-hoc comparisons exploring the main effect of AOI revealed that, independently of stimulus category and type, participants fixated significantly longer on the Torso compared to all other AOIs (Torso>Face: MD=434 ms, S.E.=66, *p*<.001; Torso>Left Arm: MD=457 ms, S.E.=56.2, *p*<.001; Torso>Right Arm: MD=463 ms, S.E.=55.8, *p*<.001; Torso>Leg: MD=375 ms, S.E.=49, *p*<.001).

Discussion

Using the human body as stimulus, in this study we explored aesthetic evaluations of subjects, naïve to art criticism, when viewing an artwork compared to a biological non-art stimulus sharing similar structural features. In particular, using the eye-tracking technique, we assessed whether possible differences in aesthetic judgments between an artistic representation of the human body, as in Classical sculptures (S), and images depicting real human bodies (HB) could be attributed to perceptual differences and/or to attendance to category-specific salient features.

To address this issue, we manipulated the canonical structural properties of the body in both stimulus-categories (S, HB), namely the body proportion, creating different degrees of modification (small, medium, high) and two types of modification (short torso: long legs – M1; long torso: short legs – M2). The results on the aesthetic ratings to the stimuli provided by the subjects during aesthetic judgment task (AJ) are discussed in association with their perceptual ability to recognize proportion manipulation, which was evaluated during proportion discrimination task (PD). Because of the physical similarities, all stimuli (S and HB) depicted only male bodies. The psychophysical responses were then analyzed also as a function of the subjects' gender.

The results associated with the aesthetic judgment task revealed that, overall, sculpture stimuli received higher aesthetic ratings than HB stimuli. One possible explanation for this finding is that our Italian subjects, although naïve to art criticism, were more familiar with Classical sculpture images than with HB images. In this case, familiarity would justify greater preference for sculptures. An alternative explanation comes from neuroimaging results (Di Dio et al., 2011), in which it was found that aesthetic judgment of sculpture images, compared to HB images, activated a specific sector of the right insula, its antero-dorsal sector, which is suggested to be involved in integrating emotional and cognitive information (for a review, see Kurth et al., 2010). This binding would determine a specific hedonic feeling underpinning the aesthetic experience when viewing art material, distinguishing it from that underpinning observation of non-art material.

The results for aesthetic judgment task further revealed that, in both stimulus-categories, canonical images were generally rated aesthetically higher that their modified versions. However, independently of stimulus-category, fine differences in aesthetic ratings were observed between gender groups in response to small modification stimuli. In fact, while females' aesthetic ratings significantly decreased after each level of stimulus modification (small, medium, high) with respect to the canonical images, there was no difference in aesthetic evaluation between the canonical images and their small-modified versions for the male subjects. This interaction effect suggests that males' aesthetic appraisal of the stimuli was less sensitive to subtle structural variations of the modified body proportion. This effect can be explained in terms of perceptual bias, as shown by our data for the proportion discrimination task. PD results showed that, in general, subjects' perceptual ability to discriminate the modified stimuli decreased with increasing levels of modification. However, females revealed to be better at recognizing these manipulations compared to males, who struggled identifying disproportion in small modification-type stimuli, reflecting the results obtained for the aesthetic judgment task.

Aesthetic judgment results further showed that, independently of category, females rated the canonical stimuli higher than both M1 and M2 modification-type images. In contrast, differences in aesthetic rating for males were observed only between canonical and M2 stimulus-type. These results suggest, once more, that females' aesthetic evaluation of the stimuli was generally more sensible to structural modifications of the canonical human form than males. Additionally, within sculpture images only, females rated M1 stimulus-type aesthetically higher than M2 disproportioned stimuli. This difference can be again explained in association with the results for the proportion discrimination task, showing that females' ability to recognize M1 modified sculpture images was much poorer than recognition of M2 modified sculptures. Similarly, the differences observed in aesthetic ratings between M1 and M2 for males is consistent with proportion discrimination results showing similar accuracy to identify M1 and M2 disproportioned stimuli in both stimulus-categories.

Congruence between data obtained in aesthetic judgment task and proportion discrimination task within gender groups supports the general idea that aesthetic evaluation of the human body relies on its structural properties (canonical proportion), independently of stimulus-category (art, biological non art). Between-gender differences further indicated that variations in aesthetic judgment were based the subjects' perceptual ability, with females showing to be better at identifying disproportion than males. In this respect, some studies have shown females' preference for symmetrical patterns in various species (e.g., Moller, 1992; 1993; Swaddle & Cuthill, 1994). Our data support the idea that preference for symmetry may be sensory biased, in that females are generally better at perceptual discrimination, possibly as a by-product of an evolutionary requirement for mate selection, as suggested in Enquist & Arak (1994; see also Conway et al., 2008).

Our behavioural data also showed that aesthetic judgment of the stimuli was equally affected by perceptual bias in both stimulus-categories, suggesting that the perception of structural variations does not generally change when viewing a Classical artistic representation of the human body or images depicting a real human body. However, results on aesthetic ratings showed a significant difference between stimulus-categories that cannot be explained in perceptual terms alone. The aesthetic evaluation of the human body, in fact, does not merely reflect goodness of its visible physical properties and one's ability to recognize them as shown by our behavioural data. Perception of the human body also involves automatic biologically driven processes, which guide attention to aspects of the human form conveying behavioural and social information. This idea is supported by our results on eye-gazing behaviour.

In general, the analysis of eye movements revealed a similar gazing pattern during all three tasks (observation, AJ, PD) for both stimulus categories, in that subjects attended longer to the Torso area. Average longer fixations on the Torso area may be reasonably justified by its position at the centre of the screen that is subject to repeated inspections. Interestingly, however, during AJ task, participants looked longer at Torso in canonical images than in their modified versions. This result may be plausibly explained by the fact that immediate identification of disproportion diverted attention towards more appealing visible aspects of the image. The tendency to get away from aesthetically unpleasant visible features would indirectly favour the cascade effect theory put forward in Shimojo et al. (2003). This theory suggests that a recursive process initiates when attending preferred features within an image, which are reinforced by a familiarity effect. More specifically, pleasant detected aspects are continuously explored determining, in a recursive fashion, a familiarity effect that reinforces the tendency to look at that particular aspect, ultimately determining a cascade effect whereby preference is reinforced by familiarity. In this light, the Torso area in our study was particularly explored in the canonical stimuli, which were aesthetically appraised higher than the modified versions. Its position at the centre of the screen may have then facilitated the cascade effect for the canonical stimuli compared to the modified ones.

Important differences in the exploration pattern between categories started emerging from the analysis of the interaction effects. Our results showed that, during AJ task, besides the Torso area, the most fixated area was the face. Interestingly, attention to the face was particularly pronounced when judging the aesthetics of the biological non-art stimuli (HB) relative to the sculpture images and, mainly, for the canonical stimuli, as opposed to their modified versions. Longer average fixations on the face area for HB stimuli were also found during observation task, suggesting, altogether, that this effect reflects an automatic tendency in natural settings.

Prolonged examination of the face area in HB stimuli may have a biological reason of its own. The human face, in fact, represents an extremely important communicative social cue. Faces convey information about a person's identity, sex, health, emotional state, and attitude, all elements that play a vital role in social interactions. In particular, behavioural studies of the aesthetic evaluation of facial beauty revealed that the eye-gaze direction of attended faces influences judgment of facial attractiveness and that direct gaze to the face can signal threat or indicate interpersonal attraction (Aharon et al., 2001; Adams & Klerk, 2003; O'Doherty et al., 2003; Conway et al., 2008). In accordance with this evidence, our data suggest that HB images automatically evoked biological responses that directed attention towards salient aspects of social value that are also used by individuals to appraise people's attractiveness (Jones et al., 2006; Conway et al., 2008). Conway et al. (2008), for example, showed that participants demonstrated stronger preferences for direct gaze when judging the attractiveness of happy faces than of disgusted faces, suggesting a salient role in social interaction for the appraisal of an individual state. These data suggest that the face area conveys a communicative meaning that has a social valence and that is plausibly most relevant when presented with a biological human form.

Nonetheless, several studies have shown that the face area is one of the most crucial elements of attraction when viewing a human form also when depicted in an artwork (e.g., Young et al., 1987; Wallraven et al., 2009; Graham et al., 2010; Abbas & Duchaine, 2008). Our data support the hypothesis that the attraction effect exerted by the face area is automatically evoked by biologically-driven responses in the viewer, directing attention towards salient aspects of social value.

Another interesting finding with respect to eye-gazing results during AJ task relates to the great attention devoted to the Arm area. This effect was enhanced for the biological non-art stimuli (HB). The Arm areas were not structurally manipulated in our experiment. Therefore, aesthetic evaluation cannot be ascribed to low-level visible features of the stimuli but, rather, to attention for elements conveying behaviourally relevant information associated with the portrayed implicit action. The most suitable explanation for this effect is provided by the embodied theory of perception (Freedberg & Gallese, 2007). The embodied theory of perception rests on the idea that the observer’s body plays a crucial role in the aesthetic evaluation of the stimuli. The physical involvement occurs, according to this theory, via mechanisms originating from a sensorimotor processing of the stimuli evoking a motor resonance in the beholder. In support of this hypothesis, some studies have shown a selective activation of the motor system during the observation of static images of human actions (Urgesi et al., 2006). Additionally, results from more recent studies of performing arts (Calvo-Merino et al., 2008; 2010) highlighted the role of the sensorimotor component in the spontaneous aesthetic response to dance. In these studies, increased activation of the premotor cortex was in fact shown during the observation of movements that received higher aesthetic ratings. In our study, attention to the Arm area was prevalent for the left arm. This effect was most likely a by-product of the fact that in 71% of HB images the Left Arm area most clearly portrayed an implied action.

Finally, with respect to proportion discrimination task (PD), we found no differences in gazing behaviour for sculptures and HB images. These results are not surprising since, during proportion judgment, task requirements most probably drove attention to the torso:leg relation that underwent modification and that best cued body proportion in both stimulus-categories. Additionally, our results on eye-gazing revealed no differences between males and females in the exploration pattern of the stimuli. This finding suggests that eye-gazing does not reflect differences in perceptual abilities between genders, which was revealed from our behavioural data when evaluating the aesthetics of the human body.

Concluding considerations

On the whole, the results of this study favour the idea that the aesthetic evaluation of the human body reflects a perceptual bias towards its structural physical properties and is therefore subject to the observers' ability to detect these properties. This is true independently of whether the attended stimulus is an artistic representation of the human body (as in Classical sculptures) or an image depicting a real human body (biological non-art stimuli). Additionally, our results suggest that other mechanisms, besides those merely pertaining to the low-level coding of the visible physical aspects of the body, are involved in the aesthetic evaluation of the stimuli. These mechanisms appear to be grounded on embodied processes, which would automatically drive attention to aspects of the body with social and behavioural relevance such as the face and the represented action. These mechanisms appear to play a role when evaluating the aesthetics of artworks and, most prominently, when viewing biological non-art stimuli, suggesting that the aesthetic evaluation of the human form has a strong biological drive.

2.2.2 Study 4 - A behavioural and eye-tracking study investigating the aesthetics of representational paintings

The debate on the definition of the processes that contribute to the surfacing of an aesthetic experience is very controversial. Different theoretical frames emphasize on the involvement of different processing levels in the building up of an aesthetic experience, which are all likely to contribute to the perception and judgment of the aesthetics of an artwork (Leder et al., 2004;Locher et al., 2010; Cupchik et al., 2009).

Given that aesthetic experience begins with a visual scan of the artwork, the multi-level interaction between the various processes in an aesthetic experience has been also studied exploring eye movement behaviour (Locher, 1996, 2006). Pioneering investigations into visual exploratory behaviour of paintings (Buswell, 1935; Yarbus, 1967) and subsequent studies (e.g., Antes, 1974; Mackworth and Morandi, 1967) revealed that observers do not explore the image at random, but tend to focus on specific areas. For example, high fixation densities into specific areas may reveal the most informative elements undergoing the observer's evaluation (Henderson and Hollingworth, 1999).

The study of the processes involved in the aesthetic experience has mainly focused on the analysis of the relation among the visual features of an artwork (Hekkert and Leder, 2008). In this respect, aesthetic experience appears to be influenced by factors such as contrast (Ramachandran and Hirstein, 1999), balance (Boselie ad Leeuwenberg, 1985), maximum effects with a minimum of means and symmetry (Berlyne, 1971; Jacobsen and Hofel, 2002). Computational models of visual exploration, using eye-tracking technique, have further identified the low-level properties responsible for drawing attention to specific areas of interest, representing the most salient regions of an image (Wallraven et al., 2009; Graham and Redies, 2010;Graham et al., 2010; LeMeur and Chevet, 2010). For example, it was shown that colour may contribute to one's aesthetic experience by enhancing the number of perceived elements within a composition (Martindale and Moore, 1988), ultimately increasing image complexity and contributing to the aesthetic appeal of the visual stimuli (Berlyne, 1970; Zellner et al., 2010).

Another factor that may contribute to visual saliency within a painting is dynamism. According to Arnheim (1992) the recognition of some dynamic qualities of the image is one of the most important elements of the aesthetic experience. The way in which motion in art is represented was explored by a study showing that one of the few graphic invariants in Western visual art is that representing motion in garments. In these examples, motion perception is evoked by the adoption of specific features such as orientation, curvature and convergence of lines, which represent robust graphic elements that have survived, in the Western culture, across countries and centuries (Gori et al., 2008).

While the visual features that make up the structural composition of a representational artwork enhance the perceptual weight of the key elements within it, the goal of the visual exploration (task) and the subjects' motivation may affect the exploration pattern when appraising the aesthetic value of an artwork (Berlyne, 1971; Jacobsen, 2006; Yarbus, 1967; Locher, 1995). The evidence that eye movement patterns are affected by the task comes from studies in humans on high-level scene perception (Henderson and Hollingworth, 1999) as well as from visual aesthetic studies (Locher, 1996; Zangemeister et al., 1995). Locher and colleagues (1993), for example, showed that asking participants to assess either complexity or pleasantness of abstract dot patterns affected their visual exploratory behaviour. Zangemeister and colleagues (1995) also found that exploration pattern of the same abstract and realistic artworks changed as function of task requirements (no instruction, remember content features for a recall task or concentrate on artistic aspects of the artworks).

Another factor which appears to affect visual behaviour during the aesthetic appraisal of artworks is the represented content (for example a human portrait or the representation of a landscape). In particular, it has been suggested that the exploration pattern of a painting representing a human content may substantially diverge from that imposed by the structural organization of artworks characterized by visual patterns lacking human forms. The structural composition of a painting may indeed affect the perceptual weights of the most meaningful elements (Kapoula and colleagues, 2010; Locher, 1996 ;Nodine, 1982). However, the presence of a human figure in a painting, considered of a high semantic value, is shown to strongly affect gazing pattern transcending the structural effect in artworks depicting, for example, landscapes or abstract figures (Graham et al., 2010).

In the present study we used eye-tracking techniques in the first stages of image scanning to investigate the contributions of low and high levels of processing in the aesthetic evaluation of representational painting. The low processes levels under investigation were Colour and dynamism; the higher order processing levels were the experimental task and the content of paintings.

Experimental Procedure

Participants

Forty-two Italian undergraduate students naïve to art criticism (22 female, 20 male, mean age = 22 S.D. = 3.95, range = 19-44) took part in this study. They gave their written informed consent to the experimental procedure. They did not present vision disorders that could interfere with the eye-tracking technique. The study was approved by the Local Ethic Committee (Università Cattolica del Sacro Cuore, Milan).

Visual Stimuli selection

Forty digital images of paintings, selected through a preliminary behavioural study, were presented.

Forty stimuli were selected and categorized into two content categories (human being *vs.* nature) representing, respectively, scenes including full-figure humans or landscapes. Within each category, the stimuli were further divided into static and dynamic. The following 4 sub-categories were used for this study: 10 dynamic human images, 10 static human images, 10 dynamic nature images, and 10 static nature images. A second set of stimuli was obtained by digitally converting the Colour images into black and white images. The Colour modification was carried out using a photo editing computer program (Microsoft Office Picture Manager). The aspect ratio of the paintings was preserved. Image sizes ranged from 495 x 818 to 788 x 524 pixels.

Procedure and Task

The stimuli were presented in two experimental tasks: aesthetic judgment (AJ) and movement judgment (MJ). The order of these two tasks was counterbalanced across participants. Eye-movements were recorded using an eye-tracking technique during both tasks.

Eighty stimuli (40 in the original Colour version and 40 in the modified black and white version) were presented on a computer screen in a randomized order. The presentation of the stimuli used during the eye-tracking session was created using the Tobii Studio 1.3 software (Tobii Technology AB). Each trial began with the presentation of a central black cross on a white background for 1 second, followed by the presentation of the stimulus that lasted 3 seconds. Then, a question appeared. Volunteers were instructed to answer to the task-related question by using the PC mouse. When the answer was given, the new trial started.

Participants were seated at a desk in a quite room, at a distance of approximately 70 cm from the monitor. They were told that they would be shown a series of paintings on the computer monitor while their eye-position was recorded. They were asked to answer a question on a 7-point Likert scale after the vision of each stimulus. The question was presented both at the beginning of each task and each time the answer was to be given. Each eye-tracker registration session lasted approximately 10 minutes. An initial calibration pattern was displayed to the participant before running both the eye-tracker sessions (AJ and MJ tasks).

Eye-Tracking data acquisition

Eye position was recorded using a Tobii Eye-Tracker X120 set on the desk in front of the subject, between the subject and the monitor. The X120 Eye Tracker is a stand-alone eye tracking unit that uses an infra-red based system for capturing reflections of the pupil and cornea in order to sample eye-position every 1/120 of a second. The system is accurate to less than 0.5 degrees.

Data were processed by the software through progressive aggregation levels. The fixations within a spatial proximity of 50 pixels determined the creation of clusters (see Figure 1). The cluster number represents the temporal order in which clusters were generated by the aggregation of fixations from each trial. Data were normalized with respect to the total area of images and of the size of clusters. The eye-movement indicators processed by the software (Tobii Studio 1.3) were fixations and observations. Fixations occur when a target feature of interest is positioned on the fovea for a variable period of time (averaging about 300 ms per fixation); observations occur each time a specific cluster is entered and exited. The data on these two eye-movements indicators were collected both in terms of number and duration.

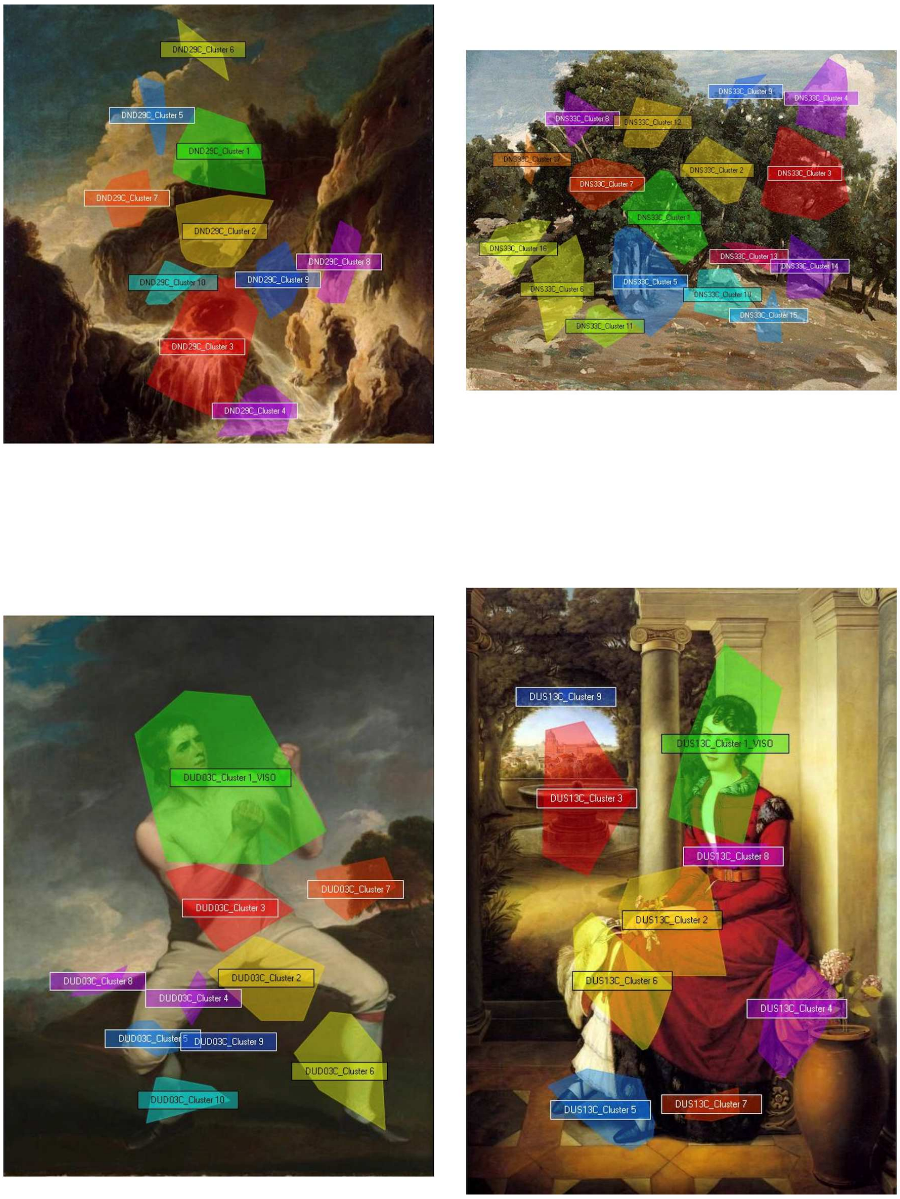

Figure 1. Examples of cluster distributions across Colour human and nature stimuli. On the left are dynamic images, on the right are static images.

Global pattern analysis. Analyses of eye-tracking data were firstly carried out within the total number of clusters formed in the paintings, corresponding to the sum of all clustered areas. For this purpose two indexes were created: 1) the total number of fixations per image, obtained by summing the number of fixations recorded for each cluster; 2) the mean duration of a fixation, obtained by dividing the total duration of fixations by the total number of fixations.

Cluster analysis. Gazing behaviour within each cluster was analyzed. Since the minimum number of clusters built across all images was 4 (range 4-20), only the first 4 clusters (Regions of Interest, ROI) formed in temporal order of exploration were considered for the cluster analysis. The variables measured in this analysis are described in Table 1.

Table 1. Description of the variables used for the cluster analysis and the relative ascribed behavioral interpretation

Measure	**Description***	**Interpretation**
Time to first fixation.	Time in seconds from when the stimulus was shown until the start of the first fixation within the cluster.	Used within the first formed cluster, it indexes the attraction power/saliency of the content of that particular cluster. The more framed the image (expected content), the longer the time to first fixation.
Fixation number.	The number of the fixations within a cluster.	Richness of details.
Fixation duration.	The length of the fixation duration in seconds within a cluster.	Salience/relevance of the content.
Observation number and duration.	Number and duration of visits to a cluster.	Capacity of a cluster to capture attention; Salience/relevance of the content with respect to the other clusters // to the task.

* As reported in the Tobii Studio 1.X – User Manual v. 1.0 (Tobii, 2008, pp. 82-86)

Latent Class Analysis. Latent class analysis (LCA) models containing one through 4 classes were fitted to the data using the 3.0 version of the Latent GOLD software (Vermunt and Magidson, 2000). Latent class analysis (LCA) is a framework based of probabilistic notions and Bayes' theorem. It aims at defining groups of subjects on the basis of the probability that each subject belongs to a specific group, investigating associations among a set of variables. This statistical method is particularly useful and powerful because it does not rely on the traditional modelling assumptions and is therefore less subject to biases associated with non-parametric data (Magdson and Vermunt, 2002). The rationale for LCA is that the observed distance between subjects with respect to a specific set of variables is reduced by the identification of *n* classes, which maximize the internal homogeneity as well as the inter-class heterogeneity.

Experimental aims

The present study aimed at answering the following research questions:

1) How do dynamism and Colour affect image exploration pattern (dynamic *vs.* static; Colour *vs.* black and white)?

2) Is there a specific exploration pattern associated with image content (human *vs.* nature)?

3) How do sensory-driven bottom-up and content-related top-down processes interact affecting the exploration pattern?

4) Is there a difference in exploration pattern between the types of task (aesthetic judgment *vs.* movement judgment) and is it correlated with the type of judgment expressed?

Results

Behavioural analysis

A 2x2x2 General Linear Model (GLM) analysis on the behavioural ratings with 2 levels of stimulus Content (human [H] *vs.* nature [N]), 2 levels of stimulus Dynamism (dynamic [D] *vs.* static [S]) and 2 levels of stimulus Colour (colour [C] *vs.* black & white [BW]) was carried out within the tasks of aesthetic judgment (AJ) and movement judgment (MJ) separately.

As far as AJ task is concerned, results revealed a main effect of Dynamism ($F_{(1\ 41)} = 10.453$; $p < .01$, $\eta^2 = .20$, $\delta = .88$; D>S) and a main effect of Colour ($F_{(1\ 41)} = 42.229$; $p < .001$, $\eta^2 = .51$, $\delta = .99$; C>BW). A significant interaction between Dynamism and Colour was also found ($F_{(1\ 41)} = 9.037$; p

$< .01$, $\eta^2 = .18$, $\delta = .84$; DC>SC) indicating that the significant difference between dynamic and static image ratings persisted only in the Colour condition. Additionally a 3 levels interaction was observed between Content, Colour and Dynamism ($F_{(1\ 41)} = 10.984$; $p < .01$, $\eta^2 = .21$, $\delta = .90$; HDBW> HSBW). More specifically, in the Colour condition, nature images received a higher AJ in the dynamic condition than in the static condition (Figure 2a); likewise, nature dynamic images were preferred over human dynamic images. In the black and white condition (Figure 2b) both these differences disappeared.

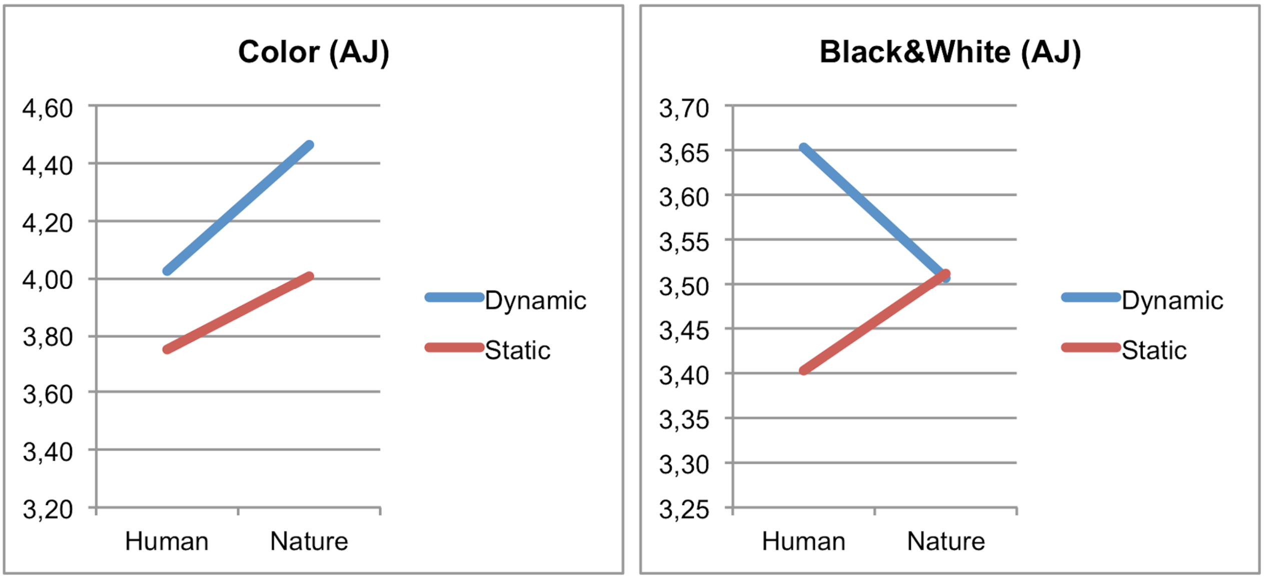

Figure 2. Aesthetic ratings in Content x Dynamism. On the left is the Colour condition (**a**), on the right is the Black and White (**b**) condition.

With reference to MJ task, results showed a main effect of Content ($F_{(1\ 41)} = 20.275$; $p < .001$, $\eta^2 = .33$, $\delta = .99$; N>H), a main effect of Dynamism ($F_{(1\ 41)} = 271.033$; $p < .001$, $\eta^2 = .87$, $\delta = .99$; D>S) - confirming our prior stimulus selection - as well as an interaction between these 2 factors. Post-hoc analyses revealed that the magnitude of the difference between human and nature in static images (ΔM=.877, $F_{(1\ 41)} = 41.969$; $p = .000$, $\eta^2 = .51$, $\delta = .99$; NS>US) was greater than the magnitude of the difference between human and nature in dynamic images (ΔM=.388, $F_{(1\ 41)} = 4.586$; $p = .038$, $\eta^2 = .10$, $\delta = .56$; ND>UD), although both of them were significant.

Eye-tracking global pattern analysis

Number of clusters. A univariate GLM analysis was conducted on the number of eye-fixation clusters as dependent variable with Content (human [H] *vs.* nature [N]), Dynamism (dynamic [D] *vs.* static [S]), Colour (Colour [C] *vs.* black and white [BW]) and Judgment task (aesthetic judgment [AJ] *vs.* movement judgment [MJ]) as independent variables. As specified in the Methods section, the clusters were automatically built by the software in relation to the distance between eye-fixations (50 pixels).

Results revealed a main effect of Content ($F_{(1\ 144)} = 25.779$; $p < .001$, $\eta^2 = .15$, $\delta = .99$; H<N) and a main effect of Dynamism ($F_{(1\ 144)} = 4.101$; $p < .05$, $\eta^2 = .03$, $\delta = .52$; D<S). More specifically, the number of clusters was smaller in human than in nature images and in dynamic than in static images.

An interaction between these 2 factors (Content and Dynamism) was also found ($F_{(1\ 144)} = 9.138$; $p < .01$, $\eta^2 = .06$, $\delta = .85$). Post-hoc analyses revealed that dynamic images presented significantly fewer clusters than static images only in nature-content stimuli ($F_{(1\ 144)} = 12.741$; $p < .001$, $\eta^2 = .08$, $\delta = .94$; DN<SN) whereas no significant differences in the number of clusters were found between dynamic and static images in the human-content stimuli. Furthermore, the effect of Content persisted only in the static condition ($F_{(1\ 144)} = 32.806$; $p < .001$, $\eta^2 = .19$, $\delta = .99$; NS>HS). In fact, the result did not show any significant difference in the number of clusters between human and nature condition in the dynamic images.

No interaction effects were observed between any of the variables and Task-type.

Total number of fixations and fixation mean duration. A 2x2x2x2 GLM was carried out on total number of fixations and mean duration of a fixation with 2 levels of stimulus Content (human [H] *vs.* nature [N]), 2 levels of stimulus Dynamism (dynamic [D] *vs.* static [S]), 2 levels of stimulus Colour (Colour [C] *vs.* black and white [BW]) and 2 levels of Judgment task (aesthetic judgment [AJ] *vs.* movement judgment [MJ]).

Results relative to the total number of eye-fixations revealed a main effect of Content ($F_{(1\ 41)} = 291.813$; $p < .001$, $\eta^2 = .88$, $\delta = 1.00$; H<N) and a main effect of Dynamism ($F_{(1\ 41)} = 256.800$; $p < .001$, $\eta^2 = .86$, $\delta = 1.00$; S<D). We found a lower number of fixations in the human-content as well as in static images than in nature and dynamic stimuli.

Additionally, a significant interaction between Content and Dynamism was found ($F_{(1\ 41)} = 116.456$; $p < .001$, $\eta^2 = .74$, $\delta = 1.00$). In human-content stimuli, static images counted a total number of fixations significantly lower than the dynamic images ($F_{(1\ 41)} = 283.669$; $p < .001$, $\eta^2 = .87$, $\delta = 1.00$; HS<HD) (Figure 3a). Likewise, in nature-content stimuli, static images counted a total number of fixations significantly lower than dynamic images, which remained always higher than the corresponding values in the human-content condition ($F_{(1\ 41)} = 10.491$; $p < .01$, $\eta^2 = .20$, $\delta = .86$; NS<ND). A significant interaction between Dynamism and Colour was further found ($F_{(1\ 41)} = 5.030$; $p < .05$, $\eta^2 = .11$, $\delta = .60$). The difference in the number of fixations between Colour and black and white images was observed only for dynamic stimuli, disappearing for the static images ($F_{(1\ 41)} = 8.886$; $p < .01$, $\eta^2 = .18$, $\delta = .83$; CD > BWD) (Figure 3b).

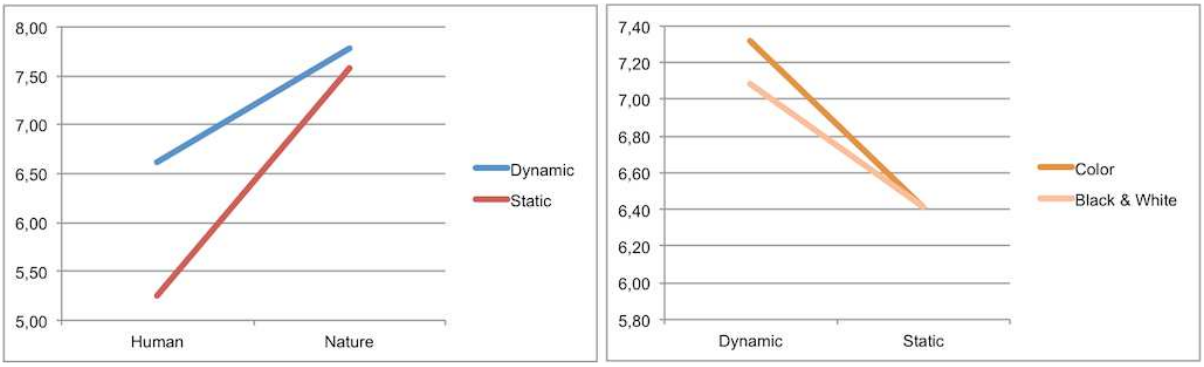

Figure 3. Total number of fixations in (**a**) Content x Dynamism and (**b**) Dynamism x Colour interactions

Finally a significant interaction between Task and Colour was found ($F_{(1\ 41)} = 5.711$; $p < .05$, $\eta^2 = .12$, $\delta = .65$). During AJ task the number of fixations was significantly higher for the Colour images than for the black and white images ($F_{(1\ 41)} = 10.112$; $p < .01$, $\eta^2 = .20$, $\delta = .87$; CAJ > BWAJ) whereas no difference was found in the number of fixations between Colour and black and white images during MJ task.

Considering the mean duration of a single-eye-fixation per image, the observed results were complementary to the results described above on the total number of fixations. In fact, significant main effects were found for stimulus Content ($F_{(1\ 41)} = 125.805$; $p < .001$, $\eta^2 = .75$, $\delta = 1.00$; H>N) and stimulus Dynamism ($F_{(1\ 41)} = 156.831$; $p < .001$, $\eta^2 = .80$, $\delta = 1.00$) S>D). Specifically, eye-fixation was on average longer on human-content images than on nature-content images and on static images than on dynamic images.

Additionally, significant interactions were found between Content and Dynamism ($F_{(1\ 41)} = 162.855$; $p < .001$, $\eta^2 = .80$, $\delta = 1.00$) as well as between Dynamism and Judgment task ($F_{(1\ 41)} = 14.402$; $p < .001$, $\eta^2 = .26$, $\delta = .96$). In particular, a significant difference in Dynamism was observed only for human-content stimuli, where static human images were observed on average with longer fixations than dynamic images ($F_{(1\ 41)} = 197.753$; $p < .001$, $\eta^2 = .83$, $\delta = 1.00$; HS>HD). On the other hand, there was no difference between static and dynamic nature-content images. A further post-hoc analysis revealed that mean fixation was significantly longer for the dynamic images in MJ task than in AJ task ($F_{(1\ 41)} = 10.011$; $p < .01$, $\eta^2 = .20$, $\delta = .87$; MJD>AJD).

Eye-tracking cluster analysis

As specified in Methods session, analyses were carried out considering only the first 4 clusters (ROIs) formed in temporal order of exploration, which corresponded to the minimum number of clusters present in all images.

ROI analysis was carried out on the 4 first clusters using 2x2x2x2 GLM models with 2 levels of stimulus Content (human [H] *vs.* nature [N]), 2 levels of stimulus Dynamism (dynamic [D] *vs.* static [S]), 2 levels of stimulus Colour (Colour [C] *vs.* black and white [BW]) and 2 levels of Judgment task (aesthetic judgment [AJ] *vs.* movement judgment [MJ]).

Cluster size. Table 2 (see Appendix) shows clusters size as a function of the percentage of area covered with respect to the total area of the image.

Results showed a main effect of stimulus Content ($F_{(4\ 141)} = 14.773$; $p < .001$, $\eta^2 = .30$, $\delta = 1.00$; N>H): ROIs extension was significantly greater in nature-content images than in human-content paintings.

Number and duration of fixations and observations. ROI analysis was carried out within each of the 4 first ROIs considering the following indexes: time to first fixation, fixation number and duration, observation number and duration.

In ROI 1, 2 and 3 results showed a main effect of stimulus Content (H>N): in all the three ROIs the fixations number and duration as well as the observations number were always higher in human-content than in nature-content images. Additionally, a main effect of Dynamism was also found for the first three ROIs (S>D). However, while in ROI 1 fixations and observation number and duration were higher in static images than in dynamic images, these effects reversed in ROI 2 and 3 (D>S). A similar trend was observed for the factor Colour in ROI 1 and 3 only with respect to fixation and observation duration. In fact, in ROI 1 we found a longer duration of fixations and observations in black and white images than in Colour images; this effect reversed in ROI 3. A higher number of fixations in black and white images than Colour images in ROI 1 was also found.

As far as the time-to-first-fixation is concerned, results showed a main effect of Content: the time necessary to enter into the first cluster was longer in human-content than in nature-content stimuli ($F_{(1\ 41)} = 32.475$; $p < .001$, $\eta^2 = .44$, $\delta = 1.00$; H>N).

Finally, results revealed that in the considered clusters, Judgment task affected observation number but not fixation indexes. Specifically, results showed a main effect of Task (AJ>MJ) in the observations number in ROIs 1 ($F_{(1\ 41)} = 8.080$; $p < .01$, $\eta^2 = .17$, $\delta = .79$) and 3 ($F_{(1\ 41)} = 7.036$; $p < .05$, $\eta^2 = .15$, $\delta = .74$).

Interaction analyses for each considered ROI and relative statistic values are summarized in Table 3 (see Appendix).

*Content*Dynamism*. A Significant interaction was found between Content and Dynamism in the first three ROIs. Also in this case the effect of the interaction reversed from ROI 1 to the other two ROIs. In fact, in ROI 1 the number and duration of fixations was higher in human static images than in human dynamic images, while in ROIs 2 and 3 these indexes were higher in human dynamic images than in human static images.

*Content*Colour.* Significant interactions were found between Content and Colour. Specifically, results revealed that, in ROI 1, black and white images received a higher number of fixations than Colour paintings only in nature-content and not in human-content images. Conversely, in ROI 2, the number of fixations and the duration of fixations were higher in Colour images than in black and white images only in human-content and not in nature-content stimuli.

*Dynamism*Colour*. Significant interactions were found between Dynamism and Colour. More specifically, in ROI 1, black and white images showed longer fixation duration than Colour images only for dynamic paintings. On the contrary, in ROI 2, fixation number was higher in Colour than in black and white images, again only in dynamic stimuli (and not in static stimuli).

*Judgment*Content.* Significant interactions were found between Content and Task only in ROI 1 ($F_{(1\ 41)}$ = 8.104; p < .01, η^2 = .17, δ = .79). The number of fixations was higher during AJ than during MJ task in human-content images only.

*Judgment*Dynamism.* Significant interactions were found between Dynamism and Task. In particular, in ROI 1, static images were observed with more ($F_{(1\ 41)}$ = 10.612; p < .01, η^2 = .21, δ = .89) and longer ($F_{(1\ 41)}$ = 14.863; p < .001, η^2 = .27, δ = .96) fixations during AJ than during MJ task. Conversely, dynamic images were observed with longer fixations during MJ than during AJ task ($F_{(1\ 41)}$ = 36.803; p < .001, η^2 = .47, δ = 1.00). Influence of movement on AJ task during the exploration of dynamic images was observed also for ROI 2 in terms of more ($F_{(1\ 41)}$ = 6.287; p < .05, η^2 = .13, δ = .69) and longer fixations ($F_{(1\ 41)}$ = 13.434; p <.01, η^2 = .25, δ = .95) than in static images.

Content Analysis and Latent Class Analysis (LCA)

Focusing only on human-content paintings, an analysis was carried out on content of each ROI which was defined on the basis of a qualitative description of the portion of the body bounded by the ROI considered (face, limbs, trunk or mixed content – face+limbs or face+trunk –, not on human body). Results showed that the face area was the first clustered area (ROI 1) in the 61,3% of the cases; this value rose to 92.6% if also considering the content of ROI 2. Additionally, results revealed that the content mostly portrayed in the remaining 3 ROIs represented the limbs, on average, in 46% of the cases.

We carried out a latent class analysis (see Experimental Procedure for details) based on the variables Dynamism (static *vs*. dynamic) and Judgment task (aesthetic *vs*. movement) to identify the presence of content-driven exploration patterns considering the first four ROIs on human-content paintings. In other words, we intended to verify the presence of different explorative approaches focusing attention on the specific contents of the human body portrayed in the first four ROIs. In particular, LCA was fitted to the first four ROIs contents, which could vary between face, limbs, body and mixed contents (limbs+face or limbs+trunk).

In the first LCA the independent variable Dynamism (dynamic *vs.* static) was used as active covariate. Active covariates are predictors of the probability to belong to the latent classes. Considering the unexplained amount of the association among the variables (L^2) and the explanative parsimony as selection criteria of the model, the best model was given by the 2-class model (L^2=213.539 p=1 , Npar =34). The R^2 values indicated that only the variance of the first two indicators (image clusters) was significantly explained by this 2-class model. In particular the model explained 22% and 31% of the variance respectively of the first and the second ROI. The covariate Dynamism significantly predicted the 2-class distinction. In fact, 73% of static images showed the predominance of face as content of the ROI 1, with a conditional probability (CP) equal to .71. This was followed by limbs as content of the ROI 2 (CP=.75). Eighty % of dynamic images showed an homogeneous distribution of choice among limbs (CP=.28), body (CP=.31) and mixed content (CP=.29) for the ROI 1, and a predominant choice of mixed content (CP=.61) for the ROI 2.

A LCA with the independent variable Judgment task (aesthetic *vs.* movement judgment) as active covariate did not show any significant effect of this predictor.

Correlation Analysis

Correlations were carried out between aesthetic or movement behavioural ratings and eye-tracking variables. Significant correlations were found only with respect to clusters covering the face area in human images. In particular, correlations were observed between movement rating and number and duration of fixations (r=.309, *p*<.05; r=.324, *p*<.05, respectively) and between movement rating and duration of observation (r=.415, p<.01). The higher these indexes, the greater the movement evaluation.

Discussion

The main aim of this study was to investigate how low and high-order factors may affect gazing behaviour while subjects' appraised the aesthetics and gave a dynamism judgment of representational paintings. More specifically, we investigated exploration pattern during the observation of artworks presented in a colour and in a black and white version (Colour) and categorized as dynamic or static (Dynamism) – low-level sensory-driven processes. Images of paintings represented natural environments or human subjects (Content) and were displayed under aesthetic and movement judgment tasks (Task) – higher-level processes. For simplicity, the effects of sensory-driven processes (colour and dynamism) on eye gazing behaviour in relation to the higher-level variables (content and task-type) are discussed in separate sections.

Behavioural data

Behavioural results obtained during the aesthetic judgment task revealed that dynamic and colour images were preferred, respectively, to static images and black and white images. However, interaction analyses showed that the aesthetic rating of dynamic nature paintings dropped appreciably in the absence of information about colour. These results suggests that colour potentiates the aesthetic effect of dynamic images by possibly enriching the picture with perceptual details (increased image complexity). This idea is in line with Zellner et al. (2010), who suggested that colour, as a low-level saliency element, can increase the complexity of visual stimuli by enhancing the number of perceived elements, ultimately contributing to aesthetic experience (see also Berlyne, 1970). This effect was not observed for human-content stimuli. In fact, preference for dynamic human images was not affected by information conveyed by colour, suggesting that aesthetic evaluation of images depicting human subjects may be guided by factors other than those associated with low-level visual processing, as in the case of nature-content stimuli. A deeper understanding of this latter observation comes from our eye-tracking results.

Eye tracking data

Effect of low-level sensory-driven and high-level content-related processes

Eye-tracking analysis was based on several measures: number of clusters formed within the image, total number and mean duration of fixations within the image and within each cluster, number of observations within clusters and time to first fixation.

The results showed that images showing human-content stimuli guided visual exploration of fewer precise areas than static nature images, in which stimulus observation counted a greater number of clusters. The attraction exerted by human-content images on a small number of informative areas was independent of dynamism, while nature-content stimuli attracted attention to few specific areas only in the case of dynamic images. In other words, images depicting a human content held defined elements of attraction (attractors) compared with nature images, in which attention was directed towards a greater and more variable number of potential attractors. Since the number of attractors in human-content paintings did not change as a function of dynamism, it is likely that, in these stimuli, attractors were common in dynamic and static images, possibly sharing similar relevant features. In particular, the lack of influence of dynamism while observing human-content paintings likely betrays the fact that a human body always implies an intrinsic and natural dynamism. On the other hand, nature content is more susceptible to low-level visually-driven processes. In fact, in static nature images, the greater number of clusters observed suggests that participants continued to explore the images in search of attractors that, on the other hand, were more readily found in dynamic nature images, that probably, because of their own dynamism, presented more attractive low-level features (Arnheim, 1992).

These results are in accord with data relative to the number of total fixations across paintings as well as cluster size. As far as fixations are concerned, dynamic and colour images revealed a greater amount of perceived details than static and black and white paintings, as shown by a higher number of fixations. The smaller mean cluster size observed for human than nature paintings, on the other hand, indicates that attractors in human images captured attention on specific narrower areas than nature images and suggests, once more, that human images contained presumably more meaningful elements than nature images.

In line with this idea, the analysis of the first three clusters formed within paintings containing a human form revealed more and longer fixations compared to nature images. Additionally, greater eye-gaze returns to these clusters in human images confirm the informative value of their content with respect to the task.

The human frame orients participants toward predetermined attractors, namely the presence of a human figure in the picture drives the search for parts of the body. Automatic search for parts of the body with social and behavioural salience, such as the face and the arm areas, is likely driven by a motor resonance mechanism in the viewer (see embodied theory of perception in Freedberg and Gallese, 2007). This automatic search may then affect the time necessary to spatially identify the expected elements, as shown by data obtained from time to-first-fixation index. The time used to make the first fixation into the first cluster was, in fact, longer in human images, where the expected content is framed, than in nature images, where the potential attractors may vary into a wider range of undefined elements. In other terms, in a picture depicting natural environments, any element represents a potential attractor that requires inspection.

In dynamic human-content paintings, the most salient elements inspected were the body parts. Results of the latent class analysis (LCA) revealed that 80% of dynamic images showed an homogeneous distribution of inspections among limbs, body and mixed content (limbs+face, limbs+body) as the first attended area. In other words, in *dynamic* images attraction was exerted by body parts portraying action (see Figure 4).

Figure 4. Heat map visualization of the gaze behavior for human Colour images. On the left is a dynamic image, on the right is a static image. The red gradient indicates portions of the image observed by the totality of the sample.

Interestingly, the results of the latent class analysis (LCA) also showed an initial attention to the face region in 73% of the *static* images. This finding is not surprising. Several studies, in fact, showed that face is the first part of the body that is scanned in portraits (Wallraven et al., 2009) activating a configural visual encoding, instead of the more common analysis of individual features (Graham et al., 2010; Abbas and Duchaine, 2008; Young et alt, 1987). Attraction to face within an image is possibly guided by automatic biological drives, given that the face represents an extremely important social cue (Aharon et al., 2001; Adams and Kleck, 2003; O'Doherty et al., 2003).

Effect of low-level sensory-driven and high-level task-related processes

A further research aim was to investigate differences between exploration patterns as a function of task-type (aesthetic judgment – AJ – *vs.* movement judgment – MJ) and whether each specific exploration pattern is associated with the output of the expressed judgment (i.e., beautiful *vs.* ugly; dynamic *vs.* static).

With respect to the sole effect of task-related processes on the general exploration pattern, results associated with the number of clusters formed within the images showed that judgment tasks did not significantly affect the participants' explorative pattern. Similarly, LCA analysis showed that the attended areas (with respect to human-content only) were the same independently of whether the participants were assessing the aesthetics or the dynamics of the paintings.

During movement judgment task, cluster 1 of static images required fewer and shorter fixations than during aesthetic judgment task where, additionally, participants returned more often on cluster 1 and 3 compared to movement judgment task. This result indicates that these portions of the image, which were among the most salient in terms of represented content (see above), needed to be re-explored for the ascription of an aesthetic evaluation. In other words, the identification of cues revealing dynamism were more readily recognized and processed during movement task than during aesthetic task, in which the identification of elements useful for an aesthetic assessment involved more explicit and evaluative processes.

Effects of sensory-driven bottom-up processes on exploration pattern were observed as a function of task-type. More specifically, we found that colour images received a greater total number of fixations across clusters than black and white images in aesthetic judgment task, whereas no differences were observed in movement judgment task. The capability of colour to enrich the image of details, as already stressed in our discussion above, probably influenced participants' need for more fixations to evaluate the images aesthetically. Additionally, shorter mean fixation durations for dynamic than for static images during aesthetic judgment task indicate that the presence of dynamic elements allowed a faster aesthetic assessment. These results suggest that image dynamism facilitated the expression of an aesthetic judgment. Fixation duration was on average longer for dynamic images during movement judgment than during aesthetic judgment task, indicating, not surprisingly, that dynamic images were more significant in terms of task fulfilment. On the whole, these data suggest that task-related processes affected exploration pattern and that attraction exerted by sensory-driven processes was functional to the fulfilment of the task.

With respect to our second question, namely whether exploration pattern was associated with the expressed judgment, correlation analyses between the various eye-tracking measures and the participants' behavioural ratings hardly produced any association. In other words, eye-gazing patterns were not predictive of either aesthetic or movement assessment of the observed stimuli. This lack of correlation is coherent with the results by Heidenreich and Turano (2011) that did not show any significant link between participants' aesthetic judgments of the paintings and fixation durations or viewing time. The only noteworthy correlation was found within movement judgment task, specifically for the face area of static colour human–content paintings.

In particular, a relation was found between dynamism evaluation and number and duration of fixations and observations within the face area. The higher these indexes, the greater the dynamism evaluation. This interaction effect suggests that dynamism assessment of static images portraying human figures relied on information conveyed by colour. Most likely, similarly to what happened with nature images, colour enhanced content details that, in the case of the face region, can be translated in a more effective representation of the face expression. This information possibly helped participants to assess stimulus-dynamism when it lacked dynamic-relevant elements, such as portrayed actions. In the absence of information about action (as in static images), participants' attention was directed toward a socially salient element, i.e. the face area, in which the amount of detail cuing movement was better defined when the image was presented in a colour format.

Concluding considerations

The relationship between the processes involved in the aesthetic evaluation of a painting seems to stem from the salience of the content represented. When nature-content is represented, processes mediated by low-level visual elements such as colour, complexity and visual dynamism, appear to preferentially affect gazing behaviour. On the other hand, when the represented content includes a human subject, gazing is strongly affected by the human figure and, in particular, by those elements of the human form that convey behaviourally salient information. In static images, these elements converge into the face region; in dynamic images, the most attended regions are those portraying an implicit action. These results would support the embodied theory of perception, which rests on the automatic activation of resonance mechanisms in the viewers. These mechanisms would mediate an embodied understanding of the observed content and, possibly because of this, affect the aesthetic value of works of art. Data showing an increased aesthetic preference for dynamic images would then emphasize the relationship between embodiment and aesthetics.

3. GENERAL DISCUSSION

3.1 The embodied component of aesthetic experience

Suggestive evidence favouring the idea of an involvement of a motor-resonance mechanism in aesthetic judgments comes from our neuroimaging Studies 1 and 2, as well as from the psychophysical Studies 3 and 4 above described. In Study 1, the observation of Classical and Renaissance sculptures, although depicted in a bi-dimensional image viewed under an unnatural context like that of an MRI scanner, elicited activation of the ventral premotor cortex and of the posterior parietal cortex. These activations suggest motor resonance congruent with the implied movements portrayed in the sculptures and underpinning an embodied comprehension of the observed objects. In other words, we do not see an artwork only with our eyes – and our visual system – but also experience it with our body as the repository of our potentialities for action.

Embodied mechanisms subserve biologically-driven processes, which would automatically guide attention to aspects of the stimuli with social and behavioural relevance. This consideration finds support in the neuroimaging and psychophysical results of Study 2 and 3, where we compared aesthetic evaluations when viewing human bodies represented as artworks (art category) and images of real human bodies (biological non-art category). In Study 2, the aesthetic judgment of the real human body figures determined an enhanced activation, compared to sculpture images, in the superior temporal sulcus (STS). This area is recognized as part of the mirror system it being involved in the coding of movements of body parts during observation. Additionally, the eye gazing results of Study 3 showed that, during observation and aesthetic judgment tasks, subjects fixated longer on the face and arm areas of the stimuli, particularly of the real human body figures. Prolonged fixations on these specific regions of the body again suggest that embodied mechanisms, besides those merely pertaining to the low-level coding of the visible physical aspects of the body, are also involved in the aesthetic evaluation of the stimuli.

The power of the human form to evoke in the observer a meaning associated with the implied action and, possibly, intention of the represented figure, also when represented in an artwork, was particularly evident in our last eye-tracking study. The results of Study 4, where we confronted gazing pattern during the aesthetic and dynamism judgment of human and nature-content paintings, showed that, when nature-content is represented, gazing behaviour was particularly affected by low-level visual elements such as colour and complexity. On the other hand, when the represented content includes a human subject, motor-resonance mechanisms seem to prevail over low-level sensory-driven processes in guiding the observers' explorative pattern. More specifically, when a human being is portrayed in a painting, gazing behaviour is mostly focused on the human figure, independently of contextual elements also depicted in the image. In particular, when judging the aesthetics of the image, attention is given to the face area, whereas dynamism ascription appears to be strongly guided by attention to features portraying actions. In this respect, our results favour an alternative interpretation of dynamism that differs from the classical description of low-level sensory-driven processes, yet recognized for nature-content paintings: When a human subject is present in an image, the recognition of dynamism shifts from a visual decoding of perceptual elements to an embodied processing of the image semantics defined by the represented actions.

Our data show that dynamism is strongly associated with aesthetic preference. If a human form is depicted in an artwork, dynamism perception is conveyed by aspects of the body representing the implied action. The question then arises of what vehicles dynamism and beauty perception in artworks representing contents other than the human body, such as nature. Is dynamism in paintings of natural scenes a sole effect of visual complexity, as our data suggest and, if so, in what terms is it coded? In terms of a possible physiological explanation, in which dynamism perception is associated with eye gazing variables, we hypothesized that, if perception of dynamism is a proprioceptive epiphenomenon elicited by eye-movements, indexes, such as number of fixations, should increase as a function of dynamism judgment. Behavioural data obtained from movement judgment task already indicated the lack of association between physiological measures and dynamism judgment in nature-content images. Additionally, analysis of physiological data alone showed that dynamic nature stimuli were characterized by a fewer number of clusters (narrow explorative behaviour) than static stimuli and by equal number of fixations, convincingly indicating that eye-movements did not affect the perception of dynamism in nature image. Perhaps, even when contemplating a waterfall, embodiment is relevant. As the German art historian Heinrich Wolfflin suggested (1886) "…as human beings with a body that teaches us the nature of gravity, contraction, strength, and so on, we gather the experience that enables us to identify with the conditions of other forms". Although very appealing, at this stage, these considerations remain only theoretical.

3.2 The hedonic value of aesthetic experience

With the aim to investigate, from a neuro-cognitive perspective, the fundamental human ability to value beauty in art, the first main question that we addressed is whether there is an objective beauty, i.e., if objective parameters intrinsic to works of art are able to elicit a specific neural pattern underlying the sense of beauty in the observer. The results of Study 1 gave a positive answer to this question. The presence of a specific parameter (i.e., the golden ratio) in the canonical Classical sculpture images we presented determined brain activations different from those where this parameter was violated (modified stimuli). The spark that changed the perception of a sculpture from "ugly" to beautiful appears to be the *joint* activation of specific populations of cortical neurons responding to the physical properties of the stimuli and of neurons located in the anterior insula.

The activation of the right anterior insula in association with the objective cannons of beauty in Classical sculptures, relative to sculptures whose proportions had been modified, was interpreted as the neural signature underpinning hedonic response during aesthetic experience. With the aim of exploring whether this specific hedonic response is also present during the observation of non-art biological stimuli, in a second fMRI study (Study 2) we compared the activations associated with the aesthetic appraisal of Classical sculpture images to those associated with the aesthetic appraisal of real human bodies represented by photographs of young athletes. The imaging results showed an overall similar cortical activation pattern at the viewing of the two stimulus categories. However, direct comparison between art and biological non-art stimuli revealed that the anterior sector of right dorsal insula was selectively activated for artworks and – crucially – not when appraising the aesthetics of real human body images. This result indicates that the hedonic value associated with aesthetic experience for artworks is distinct from that characterizing the aesthetic appraisal of biological non-art stimuli.

The hedonic response to art stimuli, mediated by insular activation, was particularly strong, in our studies, during observation condition, namely when the subjects were instructed to observe the stimuli without judging them. In this respect, it is worth noting that, in an experimental context, as that of an fMRI study, it is not easy to promote the surfacing of an aesthetic experience and is therefore important to use specific instructions in order to elicit a mind-state favouring it (see also Hofel and Jacobsen, 2007). Yet, it needs to be stressed that there is a clear difference between eliciting a mind-state that may favour aesthetic appraisal and the explicit request to give an aesthetic judgment to the presented stimuli. As already argued, this request involves cognitive processes that may interfere and even overshadow the emergence of spontaneous hedonic responses associated with aesthetic experience. The results of Experiment 2 of our second *f*MRI study, as well as the results of Study 1, supported this idea, which is in accordance with Cupchik and Lazslo’s (1992) view that specific conditions are to facilitate the emergence of an “aesthetic attitude” (see also Cupchik et al., 2009). The observers’ mind-state induced by instruction is therefore vital in setting the conditions for experiencing the aesthetic quality of the stimuli.

The aesthetic judgment of an artwork, though, is only partially built on objective measures. The results of our analysis concerning what we called *subjective* beauty (Study 1) are also relevant in this respect. In the condition in which the viewers were asked to indicate explicitly which sculptures they liked, there was a strong increase in the activity of the amygdala, a structure that responds to incoming information laden with emotional value. Thus, instead of allowing their nervous centres to "resonate" in response to the observed stimuli (observation condition), when the viewers judged the stimuli according to their individual idiosyncratic criteria (explicit aesthetic judgment), that structure was activated that signals which stimuli had produced pleasant experiences in the past. It is this process that, most likely, reconciles with the reward-based theories of beauty perception during the explicit appraisal of artworks, fully discussed in the Introduction.

In conclusion, our data support the idea that both objective and subjective factors intervene in determining our appreciation of an artwork. The objective beauty can be freely and automatically accessed during the contemplation of an artwork via the intrinsic properties of the stimulus, leading to the hedonic value associated with aesthetics. This objective aesthetics does not require an a-priori knowledge about the appraised object, although it requires a proper aesthetic attitude favouring the aesthetic experience. Subjective beauty, on the other hand, appears to be significantly affected by the individual's values, knowledge and personal taste, all factors that are subject to cultural and experiential dynamics. It would be this latter dimension of aesthetics that determines most of the variability often observed among judgments.

It has often been claimed that beauty, objectively determined, does not exist because of profound subjective differences in the evaluation of what is beautiful and what is not. Although individual biases are undeniable, it is also rather implausible to maintain that beauty has no biological substrate and is merely a conventional, experientially determined concept. As Gombrich (1984) wrote, elements in a picture which determine aesthetical experience are "deeply involved in our biological heritage", although we are unable to give a conscious explanation to them. The history of art is replete with the constant tension between objective values and subjective judgments. This tension is deepened when artists discover new aesthetic parameters that may appeal for various reasons, be they related to our biological heritage, or simply to fashion or novelty. Still, the central question remains: when the fashion and novelty expire, could their work ever become a permanent patrimony of humankind without a resonance induced by some biologically inherent parameters?

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APPENDIX – TABLES

Study 1

Table 1-S1. Brain activity reflecting the common effects of Canonical and Modified images *vs*. baseline across conditions (observation; aesthetic judgment; proportion judgment).

Brain structure		Sphere	Maxima x y z	Z	p. corr (vx)
Occipital Lobe					
	Inferior occipital gyrus (LO)	L	-45 -84 -6	Inf	0.000
		R	38 -88 -10	Inf	0.000
	Middle occipital gyrus	L	-32 -96 -6	Inf	0.000
		R	28 -92 0	Inf	0.000
		R	30 -92 -2	Inf	0.000
		R	50 -78 -8	7.82	0.000
Parietal Lobe					
	Supramarginal gyrus	R	64 -20 38	5.08	0.006
Frontal Lobe					
	Middle frontal gyrus	R	38 0 54	5.49	0.001
		R	38 -2 54	4.89	0.015
		R	38 0 52	4.65	0.041
	Inferior frontal gyrus	R	50 14 24	7.32	0.000
		R	52 14 24	5.36	0.002
		R	45 40 8	5.33	0.002
		R	50 34 18	5.25	0.003
		R	48 35 14	5.24	0.003
	Precentral gyrus	R	50 10 12	6.21	0.005
		R	54 8 42	4.84	0.019
	Precentral gyrus	L	-56 2 42	4.58	0.036
		L	-50 8 30	4.62	0.047
		L	-52 6 26	4.56	0.05
	Supplementary motor area	-	0 10 52	6.36	0.000
	Supplementary motor area	R	4 16 48	5.16	0.005
		R	2 16 50	6.01	0.000
		R	14 8 58	5.21	0.004
Subcortical/insula					
	Ippocampus	R	24 -32 -6	5.49	0.001
		R	22 -32 -6	5.35	0.002
	Ippocampus	L	-22 -32 -6	6.14	0.000
				4.92	0.013
	Insula	R	36 20 -6	5.05	0.008
	Insula	L	-34 24 -4	5.58	0.001
Cerebellum					
	Cerebellum 4-5	R	32 -34 -28	4.81	0.021

Table 2-S1. Brain activity reflecting the main effect (a) and the simple effect (b) of Canonical *vs.* Modified images.

Brain structure	Sphere	Maxima x y z	Z	p. corr Cluster level
a Main effect (C-M)				
Medial parietal lobe/Precuneus	R	12, -52, 46	3.79	0.04
	L	-2, -42, 58	3.21	
Posterior cingulum	R	8, -52, 30	3.33	
Inferior occipital gyrus	R	30, -94, -8	3.75	0.0001
Lingual gyrus	R	16, -66, -6	3.56	
Cuneus	L	-4, -78, 30	3.55	
Inferior frontal gyrus	R	44, 42, 20	3.65	0.03
Middle frontal gyrus	R	30, 40, 30	3.65	
b Simple effect Observation (C-M)				
Anterior insula/frontal operculum	R	36, 22, 16	3.86	0.016
Middle frontal gyrus	R	38, 36, 20	3.62	
Superior frontal gyrus	R	18, 44, 26	3.31	

Table 3-S1. Brain activity reflecting main effect (a) and interaction (b) of judged-as-ugly *vs.* judged-as-beautiful images.

Brain structure	Sphere	Maxima x y z	Z	p. corr Cluster level
a Main effect				
Precentral gyrus	L	-36, -14, 60	4.68	0.0001
Postcentral gyrus	L	-38, -28, 52	4.34	
b Interaction (stimulus by condition)				
Precentral gyrus	L	-36, -12, 58	4.35	0.003
Postcentral gyrus	L	-40, -34, 56	3.88	
Inferior parietal lobule	L	-50, -26, 40	3.82	
	L	-52, -32, 52	3.34	

Study 2

Table 1-S2. Brain activations reflecting the common effects of Canonical and Modified stimuli (pulled together) *vs*. baseline across conditions (observation and aesthetic judgment) observed in *Experiment 1* for **a.** Sculpture and **b.** Real Human Body images. The statistical significance refers to P-FWE corr <0.05 at the voxel level.

a. Sculpture images

Brain structure		Sphere	Maxima x y z	Z	p. FWE-corr (vx)
Occipital Lobe					
	Sup Occipital gyrus	L	-24 -70 34	Inf	0.000
	Middle Occipital gyrus	R	30 -70 34	Inf	0.000
Temporal Lobe					
	Middle Temporal gyrus (post)	L	-50 -68 6	7.38	0.000
	Inferior Temporal gyrus	R	50 -58 0	Inf	0.000
Parietal Lobe					
	Inf Parietal lobule / Intraparietal sulcus	L	-36 -52 48	6.20	0.000
	Sup Parietal lobule (post)	L	-22 -68 56	Inf	0.000
	Angular gyrus	R	24 -66 54	Inf	0.000
Frontal Lobe					
	Middle Frontal gyrus	R	50 40 14	Inf	0.000
	Inf Frontal gyrus	L	-48 14 30	5.31	0.005
		L	-52 26 26	5.25	0.001
	Inferior Frontal gyrus/p. opercularis	R	46 6 28	Inf	0.000
	Precentral gyrus	R	44 2 52	6.09	0.000
		L	-46 -2 46	5.82	0.000
	Pre-SMA	L	-4 12 52	Inf	0.000
		R	5 4 55	5.19	0.001
Subcortical/insula					
	Hippocampus	L	-16 -32 -4	Inf	0.000
		R	16 -32 -2	Inf	0.000
	Parahippocampal gyrus/Amygdala	L	-18 -8 -18	5.21	0.001
	Amygdala	R	20 -4 -18	5.77	0.001
	Insula	R	32 18 4	4.93	0.005
	Inf Frontal gyrus/pars orbitalis	L	-36 20 -6	4.42	0.030
Cerebellum		L	-38 -50 -22	Inf	0.000
		R	38 -48 -22	Inf	0.000

b. Real Human Body images

Brain structure		Sphere	Maxima x y z	Z	p. FWE-corr (vx)
Occipital Lobe					
	Sup Occipital gyrus	L	-24 -70 36	7.65	0.000
	Middle Occipital gyrus	L	-30 -76 22	6.53	0.000
		R	30 -70 34	Inf	0.000
Temporal Lobe					
	Middle Temporal gyrus	L	-50 -68 6	7.22	0.000
		R	50 -66 14	7.43	0.000
	Inf Temporal gyrus	R	52 -56 -4	Inf	0.000
		L	-46 -60 -6	7.12	0.000
Parietal Lobe					
	Sup Parietal lobule	L	-26 -68 56	Inf	0.000
		L	-12 -80 48	6.44	0.000
		R	26 -66 56	Inf	0.000
	Precuneus	R	14 -74 52	7.83	0.000
	Angular gyrus	R	30 -52 44	Inf	0.000
	Inf Parietal lobule	L	-36 -52 46	6.38	0.000
Frontal Lobe					
	Inf Frontal gyrus/ pars triangularis	L	-50 26 26	5.34	0.000
		L	-44 16 32	5.03	0.000
		R	44 32 16	6.23	0.000
	Middle Frontal gyurs	R	50 40 16	7.24	0.000
	Inf Frontal gyrus/ pars opercularis	R	46 6 28	Inf	0.000
	Precentral gyrus	R	42 2 54	5.51	0.000
		L	-30 -4 48	5.01	0.000
	Supplementary motor area	L	-4 10 54	Inf	0.000
	Middle Cingulate cortex	L	-4 22 42	5.37	0.000
Subcortical					
	Hippocampus	L	-16 -34 -4	Inf	0.000
		L	-16 -8 -18	5.70	0.000
		R	18 -32 -0	Inf	0.000
	Amygdala	R	18 -6 -16	7.02	0.000
Cerebellum		L	-38 -50 -22	Inf	0.000
		R	38 -48 -22	Inf	0.000

Table 2-S2. Brain activity reflecting the effect of stimulus **a.** CATEGORY (canonical sculpture and canonical real human body images) and **b.** TYPE (canonical and modified) for the two conditions (O= Observation; AJ= Aesthetic Judgment) in *Experiment 1*; SC= Sculpture Canonical; SM= Sculpture Modified; HBC= real Human Body Canonical; HBM= real Human Body Modified. The reported statistical significance is at cluster level and refers to activations significant (P-FWE corr <0.05) at the cluster and/or voxel level.

Contrast	Condition	Brain structure	K_E	p. FWE-corr Cluster level	Z	Sphere	Maxima x y z
a. Effects of CATEGORY							
SC-HBC	O + AJ	Fusiform gyrus	292	0.000	5.26	L	-30 -36 -18
					4.49	L	-26 -56 -14
			190	0.001	4.63	R	34 -46 -10
					4.08	R	28 -56 -8
	O	Fusiform gyrus	502	0.000	5.55	R	30 -46 -14
					4.10	R	28 -56 -10
			390	0.000	5.21	L	-26 -42 -16
					5.05	L	-32 -38 -20
	AJ	Insula	77	0.074	4.99	R	38 26 10
HBC-SC	O +AJ	Thalamus	134	0.006	4.42	R	2 -12 14
	AJ	Mid Temporal gyrus/STS	100	0.026	4.68	R	44 -50 6
		Thalamus	194	0.001	4.39	-	0 -12 14
b. Effects of TYPE							
HBM-HBC	O	Amygdala	97	0.030	5.13	L	-30 -4 -14
		Inf Temporal gyrus (post)	46	0.321	5.02	L	-48 -42 -16
HBM-HBC	AJ	Inf Temporal gyrus (post)	220	0.000	4.83	R	50 -54 -6

Table 3-S2. Brain activations reflecting the common effects of Canonical and Modified stimuli (pulled together) *vs*. baseline across conditions (observation and aesthetic judgment) observed in *Experiment 2* for **a.** Sculpture and **b.** Real Human Body images. The statistical significance refers to P-FWE corr <0.05 at the voxel level.

a. Sculpture images

Brain structure		Sphere	Maxima x y z	Z	p. FWE-corr (vx)
Occipital Lobe					
	Inf Occipital gyrus	L	-38 -82 2	Inf	0.000
		R	40 -78 -4	Inf	0.000
	Middle Occipital gyrus	R	50 -64 2	Inf	0.000
		L	-24 -76 30	Inf	0.000
	Sup Occipita gyurs	L	-18 -92 10	Inf	0.000
	Calcarine ctx	L	-8 -96 -2	Inf	0.000
Temporal Lobe					
	Lingual gyrus	R	4 -88 6	Inf	0.000
		L	-8 -88 -8	Inf	0.000
	Fusiform gyrus	R	28 -88 -8	Inf	0.000
		L	-34 -58 -14	Inf	0.000
Parietal Lobe					
	Angular gyrus	R	28 -62 50	Inf	0.000
		L	-28 -60 52	Inf	0.000
	Inf Parietal lobule	L	-36 -52 56	Inf	0.000
Frontal Lobe					
	Inf Frontal gyrus/	L	-54 14 34	7.60	0.000
	pars triangularis	R	46 10 30	Inf	0.000
		R	52 38 14	Inf	0.000
	Precentral gyrus	R	46 2 54	Inf	0.000
	Inf Frontal gyrus/ p. opercularis	L	-44 4 34	Inf	0.000
	Paracentral lobule / BA6	R	6 -30 68	5.08	0.003
	Supplementary Motor Area	-	0 14 50	Inf	0.000
	Pre-SMA	R	6 16 48	Inf	0.000
	Anterior Cinguate ctx	R	4 2 28	6.74	0.000
	Sup Orbital gyrus	L	-18 60 -4	5.69	0.028
	Middle Orbital gyrus	R	26 52 -8	5.75	0.000
Subcortical/insula					
	Hippocampus	L	-22 -30 -6	Inf	0.000
		R	22 -30 -2	Inf	0.000
	Parahippocampal gyrus /	R	24 0 -20	6.36	0.003
	Amygdala	R	32 2 -22	5.40	0.003
	Insula	R	30 30 4	7.59	0.000
		L	-30 26 2	7.24	0.000
Cerebellum		L	-2484 -14	Inf	0.000
		R	38 -64 -18	Inf	0.000

b. Real Human Body images

Brain structure		Sphere	Maxima x y z	Z	p. FWE-corr (vx)
Occipital Lobe					
	Inf Occipital gyrus	R	40 -78 -4	Inf	0.000
		L	-38 -82 2	Inf	0.000
	Middle Occipital gyrus	R	30 -84 14	Inf	0.000
Temporal Lobe					
	Fusiform gyrus	L	-34 -58 -14	Inf	0.000
		R	40 -54 -16	Inf	0.000
	Lingual gyrus	R	22 -88 -8	Inf	0.000
		L	-24 -84 -14	Inf	0.000
Parietal Lobe					
	Superior Parietal lobule	L	-26 -60 52	Inf	0.000
	Angular gyrus	R	28 -62 48	Inf	0.000
Frontal Lobe					
	Inf Frontal gyrus/pars triangularis	R	52 38 12	Inf	0.000
		R	46 10 30	Inf	0.000
		L	-54 26 24	Inf	0.000
	Inf Frontal / pars opercularis	L	-40 8 28	Inf	0.000
	Pre-SMA	R	4 -30 68	4.96	0.005
	Middle Frontal gyrus (ant)	L	-36 58 2	4.61	0.023
	Sup Orbital gyrus	L	-18 60 -4	5.72	0.000
	Middle Orbital gyrus	L	-28 52 -6	4.45	0.043
Subcortical					
	Hippocampus	L	-22 -30 -6	Inf	0.000
		R	22 -30 -2	Inf	0.000
	Parahippocampal gyrus /	L	-24 0 -16	5.12	0.000
	Amygdala	L	-20 -6 -12	4.69	0.011
	Inf Frontal Gyrus /pars orbitalis	R	34 26 -2	8.60	0.000
	Insula	L	-30 26 2	7.90	0.000
Basal Ganglia					
	Globus pallidus	L	-12 -2 -2	5.34	0.001

Table 4-S2. Brain activity reflecting the effect of stimulus **a.** CATEGORY (canonical sculpture and canonical real human body images) and **b.** TYPE (canonical and modified) for the two conditions (O= Observation; AJ= Aesthetic Judgment) in *Experiment 2*; SC= Sculpture Canonical; SM= Sculpture Modified; HBC= real Human Body Canonical; HBM= real Human Body Modified. The reported statistical significance is at cluster level and refers to activations significant (P-FWE corr <0.05) at the cluster and/or voxel level.

Contrast	Condition	Brain structure	K_E	p. FWE-corr Cluster level	Z	Sphere	Maxima x y z
a. Effects of CATEGORY							
SC-HBC	O + AJ	Lingual gyrus	1011	0.000	5.86	R	10 -84 -4
		Fusiform gyrus	160	0.095	4.67	R	30 -42 -20
	O	Lingual gyrus	7565	0.000	5.87	R	16 -84 -6
					5.16	L	-16 -42 2
		Fusiform gyrus			5.23	L	-36 -44 -10
					5.02	R	30 -38 -20
		Cuneus			5.12	R	22 -66 28
					4.58	R	26 -66 50
		Insula	134	0.180	5.21	R	30 26 6
		Inf Parietal lobule	263	0.025	4.94	R	50 -34 42
		Inf Frontal gyrus / pars triangularis	531	0.001	4.63	R	42 32 16
		Inf Frontal gyrus / pars opercularis			4.54	R	36 18 32
	AJ	Cerebellum	807	0.000	5.26	R	18 -66 -14
		Fusiform gyrus			4.45	R	30 -40 -22
		Lingual gyrus			4.36	R	16 -84 -8
HBC-SC	O+AJ	Sup/Mid Temporal gyrus	297	0.017	4.79	R	64 -40 14
					4.05	R	54 -52 16
					3.44	R	58 -38 6
		Sup/Mid Temporal gyrus	429	0.004	4.79	L	-48 -64 18
					4.57	L	-52 -54 12
	AJ	Sup/Mid Temporal gyrus	228	0.054	3.98	L	-54 -52 12
					3.54	L	-46 -54 6
b. Effects of TYPE							
SC-SM	O	Inf Frontal gyrus/ Pars triangularis	253	0.051	6.47	R	38 30 0
		Insula			4.94	R	34 18 4
		Mid Temporal gyrus	46	0.458	4.28	R	60 -54 8
SM-SC	AJ	Supramarginal gryus	156	0.132	5.47	R	60 -26 44
		Ventral Premotor ctx	210	0.076	4.44	R	50 10 32
HBM-HBC	O	Ventral Premotor ctx	233	0.050	4.60	R	52 6 28
	AJ	Inf Temporal gyrus	615	0.003	6.24	R	50 -54 -6
		Fusiform gyrus			4.11	R	30 -54 -14
		Sup Parietal lobule	306	0.038	4.11	R	30 -64 30

Study 3

Table 1-S3. Summary of the main analyses and relative statistics of the behavioural results for **a.** the aesthetic judgment task and **b.** the proportion discrimination task.

a. Aesthetic Judgment task

Source	Type	Mean	SEM	Contrast	*df*	*F*	Sig. (*p*)	*partial η2*	*Power (δ)*
Category	S	3.97	.27	S > HB	1, 20	14.49	.001	.420	.95
	HB	3.38	.21						
Degree*gender					3, 60	3.01	.037	.131	.68
(females)	C	3.96	.32	C > Msm	1, 10	8.58	.015	.62	.75
	Msm	3.70	.32						
(males)	C	3.67	.32	C = Msm	1, 10	.07	.796	.071	.057
	Msm	3.65	.33						
Type*gender					2,40	6.87	.003	.256	.902
(females)	C	3.96	.32	C > M1	1, 10	7.06	.024	.414	.993
	M1	3.69	.32	C > M2	1, 10	24.98	.001	.714	.994
	M2	3.33	.32						
(males)	C	3.67	.33	C – M1	1, 10	.013	.911	.001	.051
	M1	3.67	.32	C > M2	1, 10	9.70	.011	.492	.801
	M2	3.46	.32						
Category*Type *gender					2,40	4.85	.013	.195	.770
(females)	SM1	4.15	.44	M1 > M2 (S)	1, 10	10.95	.008	.523	.846
	SM2	3.29	.37	M1–M1 (S<HB)	1, 10	5.29	.044	.346	.547
	HBM1	3.23	.30						
	HBM2	3.37	.33						
(males)	S	3.99	.42	S > HB	1, 10	8.13	.017	.448	.729
	HB	3.24	.27	M1 > M2	1, 10	13.31	.004	.57	.907
	M1	3.67	.33						
	M2	3.46	.32						

b. Proportion Discrimination task (d-prime scores)

Source	Type	Mean	SEM	Contrast	*df*	*F*	Sig. (*p*)	*partial η2*	*Power (δ)*
Degree					2,40	5.35	.009	.211	.812
	Msm	-.38	.15	Msm > Mmd	1, 20	5.81	.026	.225	.631
	Mmd	-.77	.13	Msm > Mhd	1, 20	5.88	.025	.227	.636
	Mhigh	-1.11	.18		1, 20	5.17	.034	.206	.581
Category*type					1, 20	5.57	.029	.218	.612
	SM1	-.37	.19	M1 < M2 (S)	1, 21	6.04	.023	.223	.649
	SM2	-.98	.26						
Category*Type *gender					1, 20	7.39	.013	.270	.735
(females)	SM1	-.31	.27	M1 < M2 (S)	1, 10	4.25	.066	.298	.846
	SM2	-1.12	.49	M2–M2 (S>HB)	1, 10	4.17	.068	.294	.455
	HBM1	-.35	.25						
	HBM2	-.36	.40						

Category: S = sculpture stimuli, HB = real human body stimuli; Degree of modification: C = canonical (no modification), Msm = small modification, Mmd = medium modification, Mhigh = high modification; Type of modification: M1 =long legs : short torso, M2 = short legs: long torso; SM1, SM2 = modification type 1 and 2, respectively, for sculpture stimuli; HBM1, HBM2 = modification type 1 and 2, respectively, for real human body stimuli.

Study 4

Table 2-S4. Clusters size (%) in image representing human *vs*. nature content

	Human				**Nature**			
Cluster	Minimum	Maximum	Mean	SD	Minimum	Maximum	Mean	SD
cluster 1	.153	9.507	3.25	1.516	.933	10.881	4.415	2.051
cluster 2	.277	6.7	3.268	1.267	.527	10.385	4.00	1.841
cluster 3	.168	5.298	2.443	1.098	.157	8.844	2.911	1.960
cluster 4	.099	5.396	1.918	1.151	.108	6.768	2.584	1.516

Table 3-S4. GLM 2-ways interaction for the 4 first ROIs of fixations

		Category*Dynamism				***Category*Color***			***Dynamism* Color***		
Indexes	***ROI***		*F*	*df*	*P*		*F*	*p*		*F*	*p*
Fixation number	1	SH>DH	81.03	1,41	<.001	BWN>CN	17.6	<.001	-		
	2	DH>SH	113.4	1,41	<.001	CH>BWH	4.7	<.05	CD>BWD	9.4	<.01
	3	DH>SH	37.7	1,41	<.001	-			-		
	4	-				-			-		
Fixation duration	1	SH>DH	278.2	1,41	<.001	-			BWD>CD	49	<.001
	2	DH>SH	100.9	1,41	<.001	CH>BWH	6.9	<.05			
	3	DH>SH	58.6	1,41	<.001	-			-		
	4	-				-			-		