INTRODUCTION

Whether beauty and ugliness make up two independent and discernible pure categories or instead represent opposite extremes of one continuum still remains a philosophical debate (McConnell, 2008). This debate could significantly benefit from the study of brain function. Overall, however, only two previous neuroimaging studies have directly addressed this question including stimuli that could be straightforwardly classified as ‘ugly’ (Kawabata and Zeki, 2004; Ishizu and Zeki, 2011). In these studies, main areas involved in esthetic judgement exhibited either a linear relationship between their degree of activation and the beauty or ugliness value of a stimulus (namely, medial orbitofrontal- (mOFC) and motor cortexes, respectively), neutral stimuli being located in an intermediate position. Other brain regions were similarly activated by both beautiful and ugly relative to neutral stimuli (such as the anterior cingulate- (ACC) or the parietal cortex). Accordingly, brain activity seems to support that beauty and ugliness are not independent aesthetic categories, sharing most – if not all – of the involved neural circuits, whose pieces are activated either similarly or in opposite directions.

In the Ishizu and Zeki (2011) and Kawabata and Zeki (2004) studies the stimuli consisted in paintings or music excerpts. Strikingly, the same stimuli judged as ugly by some subjects were judged as beautiful by others, and vice versa. This might result as problematic for a plain elucidation of whether beauty and ugliness are actually related or independent in the human brain. In this regard, rightful ugliness might not have been compellingly ensured, but rather ambiguous and highly variable across individuals. It appears to us that by using more natural stimuli for which the human brain is importantly and specifically wired, judgements on ugliness or beauty could be more consistent, less subjective, and less prone to cultural and educational factors. The use of natural stimuli that can be judged as extremely ugly or extremely beautiful in a more consistent basis could help to reveal the existence of separated neural circuits for both types of esthetic judgements, if they exist.

Two of these natural stimuli that could accomplish the criteria of being judged as extremely ugly or beautiful are faces and bodies. Human faces and bodies entail biologically and socially significant items, for which ugliness might be expected to be more straightforwardly valued. In this regard, although not impossible, a given body or face would hardly be found to be classified as very ugly by some people and very beautiful by others.
If esthetics is a product of the human brain, and considering that the latter is highly social (or hyper-social) (e.g., Flinn et al., 2005), the evaluation of others’ esthetic values appears as a basic building block for beauty and ugliness as meaningful semantic concepts.

Human faces usually classified as ‘unattractive’ or ‘non-beautiful’ have been employed in several studies affording the neural basis of the judgement of beauty (e.g., Winston et al., 2007; Chatterjee et al., 2009; for a comprehensive neural model and review, see Ishai, 2008). However, the term ‘unattractiveness’ is not necessarily synonymous of ‘ugliness’; that someone or something is unattractive or non-beautiful can be either an ambiguous categorization, or meaning that it is simply devoid of beauty. This would be the case even if ‘neutral’ stimuli have also been present. Extreme and unmistakable categories are needed. A similar arguing applies to studies on human bodies in the neuroimaging milieu (for a comprehensive review, see Cacioppo et al., 2008); further, these studies have rather focused on sexual desire and lacked genuinely ugly samples.

The present study included as judged material faces and nude bodies that accomplished the criteria of being categorized as very ugly or very beautiful. This way, we approached the concepts of ugliness and beauty in the human brain in rightly extreme ways and as established on biologically and socially meaningful stimuli. Our approach also involved some degree of abstraction within these concepts, as the esthetic judgements concerned to either bodies or faces indistinctly, as this was unpredictable and not relevant variable for the task. The same applies to the gender of the stimuli. In consequence, particularities specifically related to either facial or body judgements or to sexual attraction would largely be overridden.

Given the particular task and the choice of stimuli used in the present study, several significant factors are expected to be in play, most likely impacting our results. One concerns the emotional dimensions (valence and intensity) presumably elicited by the esthetic evaluation of socially and biologically relevant stimuli. Seeing bodies of others, as well as own body, convey a number of activations related to emotional responses (e.g., Vocks et al., 2010), particularly implying the limbic regions—mainly, the amygdala—as well as other areas related to higher levels of attention. The same principles should apply to faces in our study, as they were equally relevant. Accordingly, we expect limbic activations as main neural mechanisms implied in our study. Limbic responses on the other hand are also expected to vary as a function of the esthetic values of the stimuli. Both beauty and ugliness are known to trigger highly intense emotions (Rawlings, 2003; Silvia, 2005) and though in a first glance they might represent positive and negative valences, respectively (see, e.g., Jacobsen et al., 2004), this is however not necessarily always the case, as there may be fascination with ugliness, i.e., deformation, grotesque, morbid, etc. (e.g., Eco, 2007, Rawlings, 2003). The classic assumption that activations of the amygdala relate solely to negative emotions seems no longer tenable (e.g., Winston et al., 2007), and therefore it is possible that this structure might not importantly contribute to our data. Nevertheless, other regions most usually associated with identifiable emotional valences, such as the nucleus accumbens (NAcc) for positive emotions (e.g., Sabatinelli et al., 2007) might help to better define and differentiate the valence of the emotions elicited by our stimuli.

Tightly linked to the emotional, social, and biological features commented above, an important portion of our brain activations could also relate to self-referential (normally referring to an external—or others’—viewpoint; see Pöppel et al., 2013) and self-related (internal viewpoint) processing as main mechanisms involved in the evaluation of others (Northoff et al., 2006; Pöppel et al., 2013). Evaluating others seems to imply the continuous involvement of self-referential and self-related systems located in the medial cortex of the brain, such as the ventromedial prefrontal cortex or the precuneus. Indeed, this might be a main difference between ours and other studies on esthetics, since evaluating body parts elicit different brain activations as a function of the type of representation: realistic pictures activate the precuneus, contrasting with unrealistic representations (Silveira et al., 2012), whereas photographs, but not paintings, of body parts activate ventromedial prefrontal regions including the mOFC (Lutz et al., 2013). Indeed, self-referential and self-related information seems to be continuously and automatically involved when evaluating the value of others (Li and Kenrick, 2006). It might be therefore that both the extremely ugly and the extremely beautiful stimuli in our study activate these medial regions similarly, a consequence of the strong involvement of self- vs. others-referential systems expected in our task.

Finally, and again highly related with the argumentations above, it appears expectable the involvement of the default mode network (DMN) in our study. The DMN, which conveys some of the medial cortex areas mentioned earlier (Buckner et al., 2008), is not only significantly activated during esthetic appraisal (Vessel et al., 2012; Vartanian and Skov, 2014) but also, and importantly here, in processes related with empathy (Farrow et al., 2001), theory of mind (Mars et al., 2012), and self/other distinction (Ruby and Decety, 2004). Accordingly, we expect to find the implication of the DMN in our study, as the task demands others’ evaluation while presumably involving self-referential and self-related systems.

**EXPERIMENTAL PROCEDURES**

**Subjects**

Twenty, right-handed (average handedness score of +75; Oldfield, 1971) healthy subjects (10 females) participated in the study (mean age = 21.3; SD = 3.9). They were undergraduate students, with corrected-to-normal vision, and with no history of neurological or psychiatric complaint, as declared by the participants. All the subjects declared to be heterosexual. Informed consent to participate in the study was obtained from all the subjects, who were reimbursed for their cooperation. The study was accomplished according to the Declaration of Helsinki,
and approved by the ethics committee of the University of La Laguna.

Psychophysical testing and scaling

A preliminary pool of 1800 stimuli was built consisting of 450 female faces, 450 male faces, 450 female bodies, and 450 male bodies, selected on the base of their extreme ugliness, extreme beauty, or neutrality by the experimenters. The stimuli were obtained from numerous open-access internet web pages and accomplished the criteria of directing the gaze to the viewer in the case of faces, and of being nude and displaying different positions while performing diverse activities in the case of bodies. All the people displayed were between about 20 and about 40 years of age, and none presented an apparent pathology. In the case of faces, these presented either a neutral or slightly smiling expression. The bodies were either entire, from head to feet, or at least from head to knees; their postures could never convey erotic or sexual implications. Special care was taken so that ugliness or beauty could never be confounded with obesity, thinness, or age. In this regard, both fat and thin bodies could be found among the ugly bodies, but they were never extreme cases and implied less than 10% of the ugly bodies of either gender. On the other hand, all the age ranges included were represented similarly in either group of stimuli. Using an image-editing program (Adobe Photoshop 7.0), the background details of all these stimuli were replaced with flat black, and the images normalized in terms of spatial frequency, visual area and contrast. Since several of the stimuli belonged to people from different races, brightness was not normalized, this variable being contrasted for possible between-conditions dissimilarities in final individual selections by experimental subjects (see below). The same applied to a small proportion of black and white pictures. Any superfluous features such as earrings, scarves, necklaces, tattoos, etc., were removed, but the faces always kept their hair, part of their nude neck, and their make-up (when present) whereas the bodies always kept their head, but face and sexual organs were blurred in order to keep esthetic judgement restricted to body. The size of each represented image (either face or body) was normalized for faces by measuring the distance between the center of the eyes, and for bodies by measuring the distance between the shoulders and the hips. Then, after considering these referential measures, the height and width of each stimulus could vary slightly, depending on either particular face shape configuration or the position of the body.

The edited preliminary pool was examined and rated by eight subjects (four females) other than the experimenters and participants in the experimental study. The ratings consisted in a 5-fold scale in which the stimuli could be classified as “very ugly”, “ugly”, “neutral”, “beautiful”, or “very beautiful”. From these ratings, a second pool of 840 selected stimuli was built, composed by 70 stimuli of each type (12 types, as a function of multiplying two genders – male, female – by two domains – face, body – by three esthetic judgements – ugly, neutral, beautiful). Within each of the corresponding four groups of ugly stimuli, 35 had been unanimously rated as “very ugly” and 35 as “ugly”. The same principles applied for the beautiful stimuli. Each group of 70 neutral stimuli comprised stimuli unanimously rated as neutral. When more than the necessary number of stimuli for each type reached the required ratings, the elimination of extra stimuli was performed randomly. It was never the case that a stimulus rated as ugly by some subjects was rated as beautiful by others and vice versa. Examples of the stimuli used in the present experiment can be provided upon request to the authors.

Between 4 and 7 days prior to imaging, each experimental subject (i.e., subjects to be scanned) viewed the second pool of 840 stimuli on a computer monitor. Each picture was given a score on a scale from 1 to 10 (from “very ugly” to “very beautiful”) by each subject, then arriving at an independent and individual assessment of ugly, beautiful, and neutral stimuli. Based on these psychophysical tests, a total of 16 stimuli of each type (as mentioned, 12 types, as a function of gender, domain – face or body –, and esthetic judgement), was selected for being viewed in the scanner by a given experimental subject, following her/his individual ratings, making a total of 192 pictures. In the ugly and beautiful categories, only stimuli classified by the subject as 1 and 10, respectively (occasionally, also 2 and 9, if not enough 1s and 10s were reached), were viewed in the scanner, whereas for pictures classified as neutral, only stimuli belonging to categories 5 and 6 were viewed. Analyses on the pictures chosen by the whole set of experimental subjects showed no remarkable differences between the three main esthetic conditions in visual parameters (for beautiful, neutral and ugly stimuli, respectively: average brightness in percentage of luminance was 61.8, 71.5 and 63.8; percentage of black and white pictures was 10.1, 8.9 and 7.3; race of the pictured person – percentage of white people – was 97.3, 97.5 and 90.6).

Functional Magnetic Resonance Imaging (fMRI) stimulus

Participants laid flat inside the magnet and viewed the stimuli via special stimulation glasses for MRI environments (MRI compatible eyeglasses, Visuastim, Resonance Technology, Northridge, CA, USA). This was an event-related study that followed the procedures employed in Kawabata and Zeki (2004). Accordingly, stimuli were analyzed individually (event-related) yet presented in blocks, as detailed in the following. In this design, stimuli were presented in 12 successive blocks appearing in random order, each block belonging to a different stimulus category (female faces, female bodies, male faces, and male bodies). Each block contained eight stimuli: of these, six belonged to one judgmental category and two to the other two categories. For example, a block contained eight stimuli of which six had been classified by the subject as ugly, one as beautiful, and one as neutral. The predominant judgmental category within a block was assigned randomly, and all categories appeared as
predominant equally across the 12 blocks. The stimuli and their rating (e.g., ugly, beautiful, or neutral) appeared in random order within each block. Each epoch (block) lasted 20 s, and each stimulus was shown for 2 s (no fixation required) with an interstimulus interval or around 500 ms, during which the subject fixated a central cross. Each of the stimuli was presented twice but not in the same or in subsequent epochs, making a total of 384 presentations (finally, a total of 24 blocks). The design permits event-related analyses, as the specific type of appearing stimulus and judgmental category were always highly unpredictable, while improving the blood-oxygenated level-dependent (BOLD) signals linked to the predominant judgmental category and stimulus type within a block. Participants were required to press one of three buttons in the scanner for each stimulus to indicate whether it was ugly, beautiful, or neutral. Responses could occur during the 2-s-presentation period of each stimulus as well as during the fixation time, as no explicit indication was given in this regard. Data relative to reaction times, omissions, and misclassifications – as compared to individual previous psychophysical classifications – were used as behavioral-dependent variables in the experiment. Preceding the 24 experimental blocks, the task started with a block of 20-s duration and stimuli not to be included in the study; this served both to stabilize the BOLD signal and as practice trials, the data being discarded thereafter during the analyses.

**fMRI data acquisition and analysis**

Scanning was done in a 3.0-T GE scanner (HD×, 15.x with eight channels and with gradient specifications as follows: Amplitude = 50 mT/m and slew rate = 150 mT/m × ms), equipped with a standard birdcage head coil. In a separate session, high-resolution whole-brain images were acquired from each participant using a T1-weighted three-dimensional 3DSPGR sequence (168 adjacent slices, 1-mm thickness, 228 × 228 pixel matrix per slice, TR = 11.2 ms, TE = 2.21 ms). These anatomical images were acquired prior to the functional scans, and were used to align with the functional scans. During the functional scans, the BOLD response was measured using a single-shot gradient EPI-sequence (TR = 3 s, TE = 30 ms, flip angle 90°). Horizontal images were acquired for 41 slices parallel to the AC–PC plane and covering the whole brain (2.6-mm thickness, 1-mm interstitial gap, matrix 96 × 96, field of view 260 mm, acquisition in ascending order, scan time = 483 s, number of total volumes = 161; in-plane resolution of 2.03 × 2.03 mm after interpolating the matrix by 128 × 128 in the reconstruction step).

Statistical analyses were done with SPM8 (Statistical Parametric Mapping V8 http://www.fil.ion.ucl.ac.uk/spm). The EPI images were realigned spatially, normalized to the Montreal Neurological Institute (MNI) template provided in SPM8, smoothed spatially with a 10-mm Gaussian kernel, and filtered temporally with a band-pass filter with a low-frequency cut-off period of 300 s and a high-frequency cut-off shaped to the spectral characteristics of the canonical haemodynamic response function within the SPM8. Movement correction was done by applying an affine rigid registration as part of the realignment procedure using SPM8. The realignment parameters (three shift x-y-z and three rotations) were used as confounding effects in the linear regression model in order to statistically control for the variability due to movement. Data from all 20 subjects were analyzed and combined in whole-brain full factorial, multiple regression GLM, and fixed-effects analyses. All of the event types were segregated post hoc into a 3 × 2 × 2 event-related design. The three factors were the different response conditions (ugly, neutral, beautiful), the two genders of the stimuli (female, male), and the two different stimulus domains (faces, bodies). Statistical maps were thresholded at p < 0.05, corrected for multiple comparisons family-wise error (FWE) with an extent threshold of 10 voxels. Results with p < 0.001 uncorrected were also explored.

**RESULTS**

**Behavioral data**

Table 1 displays the results of one-way repeated-measures ANOVAs for reaction times, omissions, and misclassifications separately, followed by corresponding post hoc pairwise comparisons with the Bonferroni correction. The data indicate that the neutral condition appeared more difficult than the other two conditions, as it implied significantly longer reaction times, omissions, and, notably, misclassifications. Interestingly, the two extreme esthetic conditions (ugly and beautiful) yielded always very similar values. Misclassifications in the neutral stimuli showed a slight trend for being classified as beautiful (60% of total misclassifications).

**Brain activity**

In a first approach, a full factorial analysis showed that the factor gender of the picture did not yield significant main effects nor interactions at p < 0.05. This remained the case even when splitting the sample as a function of the gender of the participant. On the other hand, at this level of analyses domain (i.e., face vs. body) showed significant main effects, but not in interaction with esthetic category. As expected (Downing et al., 2001), contrasting body vs. face yielded as main result a strong activation of the lateral occipitotemporal areas, bilaterally, extending to the parietal lobes (with peaks in the right hemisphere at 10–90 36 and 46–76 10; Kp = 18,801; p < 0.0001, corrected). Surprisingly, however, contrasting face vs. body resulted in strong activation of the primary visual areas, namely lateral inferior and mid occipital areas (BA 17 and 18) bilaterally, with peaks in the right hemisphere at 24–94 –6 and in the left at –22 to 98 –6; Kp = 176 and 122, respectively; both p < 0.0001, corrected). The absence of activation in the fusiform gyrus for this contrast, which was the expected result, might be understood in the light of the existence of strong activations for both bodies and faces within this region (Schwarzlose et al., 2005). Finally, at this level of analyses the esthetic factor yielded the strongest activations, mainly at left parietal and post-central areas. Since
our main interest was to determine in detail the cortical activity that correlates with viewing beautiful, ugly, or neutral stimuli, we charted multiple regression analyses for these esthetic dimensions whose main results are described in the following.

Table 2 shows the main results for the esthetic contrasts.

**Beautiful vs. Ugly and Ugly vs. Beautiful**

The contrast of beautiful vs. ugly stimuli produced activity in the left caudate/NAcc, the ACC and the supplementary motor area (SMA), bilaterally (cf. Figs. 1 and 2). In turn the contrast of ugly vs. beautiful produced bilateral activation in the calcarine fissure and the lingual gyrus (Fig. 2). Parameter estimates comprising the neutral stimuli were plotted in order to appreciate linear or non-linear relationships between the esthetic categories within these areas (Figs. 1 and 2). Results indicated well-defined linear relationships (i.e., neutral stimuli approximately equidistant) in which beautiful stimuli produced the highest activity and ugly the lowest one in the NAcc and the ACC. Though the difference between neutral stimuli and the other esthetic categories was not statistically significant in the NAcc even with \( p < 0.001 \), uncorrected, a significant difference in the contrast beauty vs. neutral was found in the ACC. On the other hand, calcarine/lingual areas displayed a reversed linear pattern, with ugly stimuli producing the highest activity and beautiful the lowest. Interestingly, the pattern of activations in SMA was not a linear one; rather, beautiful and neutral stimuli yielded relatively closer values, whereas ugly stimuli located at an appreciable distance below these categories. Indeed, both the contrasts Beautiful > Ugly and Neutral > Ugly showed statistically significant results in SMA bilaterally.

**Neutral vs. Beautiful and Neutral vs. Ugly**

Remarkable results were obtained in the contrasts neutral vs. beautiful and neutral vs. ugly. The former showed activations mainly in somatosensory and motor regions; namely, right precentral gyrus, parietal areas (superior, inferior, and supramarginal) most bilaterally, and the right cerebellum (Fig. 4). The contrast neutral vs. ugly exhibited activations of these same regions, but notably extended to mid and superior frontal gyri, most bilaterally, and to the left cerebellum; in this contrast, the precentral activations were mainly left. Parameter estimates for all these somatosensory and motor areas showed a somewhat sharp non-linear relationship, with neutral stimuli always highly activated and equidistant from ugly and beauty, which in turn exhibited relatively equivalent lower values (Fig. 4). The contrast neutral vs. ugly displayed other activations comprising portions of the frontal operculum and anterior insula, bilaterally, and the right inferior frontal gyrus and lateral orbitofrontal cortex (lOFC). Plotting of parameter estimates for all these regions evinced again a non-linear relationship, with neutral stimuli always over both ugly and beautiful; these in turn presented very similar values at some parts, like the right frontal operculum and the insula (left and right). This is further supported by a significant difference between beautiful and neutral stimuli with \( p < 0.001 \), uncorrected, at the right frontal operculum. Other parts (right inferior frontal region and lOFC), however, showed small differences between beautiful and ugly stimuli.

**Spatial mapping**

The contrasts of beautiful vs. neutral and ugly vs. neutral might also engender activations indicative of linear or other types of relationships between esthetic categories. The former contrast produced activations in the mOFC, the middle frontal gyrus, the three cingulate subdivisions (anterior, middle, and posterior), the precuneus, and the left angular gyrus (Fig. 3). The contrast ugly vs. neutral displayed activation in the middle cingulate. When parameter estimates were plotted (Fig. 3), we could find non-linear relationships at all these regions, except for the ACC, as already reported. Indeed, in the precuneus, posterior and middle cingulate as well as in mOFC both extreme esthetic categories (beauty and ugly) yielded comparable comparables contrasts as contrasted with neutral. Supporting this observation, the activation of the mOFC by ugly stimuli contrasted with neutral was significant at \( p < 0.001 \), uncorrected; this was not the case however for the posterior cingulate and the precuneus (the activation could nevertheless be seen increasing to \( p < 0.005 \), uncorrected). On the other hand, the angular gyrus and the middle frontal gyrus appeared more activated by beautiful stimuli than by ugly, which in turn appeared so in comparison to neutral. The contrasts between ugly stimuli and the other two esthetic categories did not yield significant results for these portions, not even with \( p < 0.001 \), uncorrected.
DISCUSSION

In the present study, male and female participants were scanned while judging the esthetics of faces and nude bodies of both genders that accomplished the criteria of being categorized as very ugly, very beautiful, or neutral. Our results showed that the factor gender of the picture did not yield significant main effects or interactions, even after splitting the sample as a function of the gender of the participant. Although it is possible that a reduction of statistical power is at the base of this result, it is also possible that the requirements of the task (in which gender or body part –i.e., face vs. body– of next stimulus was highly unpredictable in succession and overall esthetic judgement was required irrespective of gender or body part) minimized in general the possible effects of factors other than esthetics. This result would support that our task was successful in entailing some degree of abstraction within these concepts and, therefore, that our data are not straightforwardly comparable to previous literature specifically on facial or body judgements, nor to sexual attraction.

At the level of esthetic judgements, we have found positive linear relationship for the dimensions ugly-neutral-beautiful in the caudate/NAcc and the ACC, and

<table>
<thead>
<tr>
<th>Brain regions</th>
<th>L/R</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>T</th>
<th>kE</th>
<th>BA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beautiful &gt; Neutral</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Middle frontal gyrus</td>
<td>L</td>
<td>−26</td>
<td>22</td>
<td>42</td>
<td>5.08</td>
<td>71</td>
<td>8</td>
</tr>
<tr>
<td>Angular gyrus</td>
<td>L</td>
<td>−56</td>
<td>−64</td>
<td>30</td>
<td>4.59</td>
<td>140</td>
<td>39</td>
</tr>
<tr>
<td>Anterior cingulate</td>
<td>L</td>
<td>−8</td>
<td>46</td>
<td>0</td>
<td>4.30</td>
<td>56</td>
<td>32</td>
</tr>
<tr>
<td>Middle cingulate</td>
<td>2</td>
<td>−28</td>
<td>48</td>
<td>4.14</td>
<td>65</td>
<td>31</td>
<td></td>
</tr>
<tr>
<td>Posterior cingulate</td>
<td>2</td>
<td>−52</td>
<td>30</td>
<td>3.96</td>
<td>54</td>
<td>31</td>
<td></td>
</tr>
<tr>
<td>Precuneus</td>
<td>L</td>
<td>−8</td>
<td>−52</td>
<td>38</td>
<td>3.44</td>
<td>30</td>
<td>31</td>
</tr>
<tr>
<td>Medial OFC</td>
<td>L</td>
<td>−4</td>
<td>56</td>
<td>−2</td>
<td>3.35</td>
<td>56</td>
<td>10</td>
</tr>
<tr>
<td>Neutral &gt; Beautiful</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Parietal inferior</td>
<td>L</td>
<td>−50</td>
<td>−38</td>
<td>56</td>
<td>6.72</td>
<td>1605</td>
<td>40, 2, 6, 3, 4</td>
</tr>
<tr>
<td>Cerebellum</td>
<td>R</td>
<td>24</td>
<td>−62</td>
<td>−20</td>
<td>4.76</td>
<td>221</td>
<td></td>
</tr>
<tr>
<td>Parietal/supramarginal</td>
<td>L</td>
<td>−64</td>
<td>−24</td>
<td>32</td>
<td>4.36</td>
<td>123</td>
<td>40, 2</td>
</tr>
<tr>
<td>Parietal/supramarginal</td>
<td>R</td>
<td>54</td>
<td>−26</td>
<td>44</td>
<td>4.13</td>
<td>75</td>
<td>40, 2</td>
</tr>
<tr>
<td>Parietal inferior</td>
<td>R</td>
<td>36</td>
<td>−38</td>
<td>48</td>
<td>3.93</td>
<td>35</td>
<td>40</td>
</tr>
<tr>
<td>Parietal superior</td>
<td>L</td>
<td>−26</td>
<td>−56</td>
<td>46</td>
<td>3.85</td>
<td>31</td>
<td>7</td>
</tr>
<tr>
<td>Precentral gyrus</td>
<td>R</td>
<td>54</td>
<td>0</td>
<td>32</td>
<td>3.67</td>
<td>42</td>
<td>6</td>
</tr>
<tr>
<td>Beautiful &gt; Ugly</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Caudate/nucleus accumbens</td>
<td>L</td>
<td>−16</td>
<td>26</td>
<td>0</td>
<td>3.94</td>
<td>24</td>
<td></td>
</tr>
<tr>
<td>Anterior cingulate</td>
<td>L</td>
<td>−2</td>
<td>40</td>
<td>16</td>
<td>3.82</td>
<td>24</td>
<td>32</td>
</tr>
<tr>
<td>Supplementary motor area</td>
<td>L + R</td>
<td>2</td>
<td>16</td>
<td>56</td>
<td>3.56</td>
<td>36</td>
<td>8, 6</td>
</tr>
<tr>
<td>Ugly &gt; Beautiful</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Calcarine/lingual g.</td>
<td>R</td>
<td>18</td>
<td>−84</td>
<td>−4</td>
<td>4.59</td>
<td>80</td>
<td>17</td>
</tr>
<tr>
<td>Calcarine/lingual g.</td>
<td>L</td>
<td>−4</td>
<td>−92</td>
<td>0</td>
<td>3.77</td>
<td>24</td>
<td>17</td>
</tr>
<tr>
<td>Ugly &gt; Neutral</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Middle cingulate</td>
<td>−4</td>
<td>−28</td>
<td>46</td>
<td>3.84</td>
<td>25</td>
<td>31</td>
<td></td>
</tr>
<tr>
<td>Neutral &gt; Ugly</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Supplementary motor area</td>
<td>L + R</td>
<td>2</td>
<td>12</td>
<td>52</td>
<td>6.02</td>
<td>734</td>
<td>6, 8</td>
</tr>
<tr>
<td>Parietal inferior</td>
<td>L</td>
<td>−50</td>
<td>−40</td>
<td>50</td>
<td>5.86</td>
<td>918</td>
<td>40, 2</td>
</tr>
<tr>
<td>Anterior insula</td>
<td>L</td>
<td>−36</td>
<td>18</td>
<td>4</td>
<td>5.19</td>
<td>91</td>
<td>13</td>
</tr>
<tr>
<td>Superior frontal gyrus</td>
<td>L</td>
<td>−22</td>
<td>−8</td>
<td>72</td>
<td>4.76</td>
<td>108</td>
<td>6</td>
</tr>
<tr>
<td>Middle frontal gyrus</td>
<td>L</td>
<td>−46</td>
<td>38</td>
<td>22</td>
<td>4.72</td>
<td>137</td>
<td>10</td>
</tr>
<tr>
<td>Middle frontal gyrus</td>
<td>R</td>
<td>40</td>
<td>50</td>
<td>2</td>
<td>4.56</td>
<td>187</td>
<td>10</td>
</tr>
<tr>
<td>Cerebellum</td>
<td>R</td>
<td>26</td>
<td>−54</td>
<td>−26</td>
<td>4.52</td>
<td>190</td>
<td></td>
</tr>
<tr>
<td>Middle frontal gyrus</td>
<td>R</td>
<td>24</td>
<td>2</td>
<td>56</td>
<td>4.48</td>
<td>127</td>
<td>6</td>
</tr>
<tr>
<td>Anterior insula</td>
<td>R</td>
<td>34</td>
<td>22</td>
<td>2</td>
<td>4.36</td>
<td>118</td>
<td>13</td>
</tr>
<tr>
<td>Precentral/Inf. frontal g</td>
<td>L</td>
<td>−52</td>
<td>4</td>
<td>44</td>
<td>4.36</td>
<td>90</td>
<td>9, 6</td>
</tr>
<tr>
<td>Frontal operculum</td>
<td>R</td>
<td>46</td>
<td>36</td>
<td>24</td>
<td>4.20</td>
<td>224</td>
<td>46</td>
</tr>
<tr>
<td>Parietal/supramarginal</td>
<td>R</td>
<td>52</td>
<td>−32</td>
<td>44</td>
<td>4.10</td>
<td>70</td>
<td>40, 2</td>
</tr>
<tr>
<td>Parietal/supramarginal</td>
<td>L</td>
<td>−56</td>
<td>−24</td>
<td>28</td>
<td>4.08</td>
<td>69</td>
<td>40, 2</td>
</tr>
<tr>
<td>Inferior frontal gyrus</td>
<td>R</td>
<td>38</td>
<td>22</td>
<td>−12</td>
<td>4.03</td>
<td>28</td>
<td>47</td>
</tr>
<tr>
<td>Precentral gyrus</td>
<td>L</td>
<td>−36</td>
<td>−30</td>
<td>54</td>
<td>4.02</td>
<td>71</td>
<td>4</td>
</tr>
<tr>
<td>Cerebellum</td>
<td>L</td>
<td>−24</td>
<td>−72</td>
<td>−26</td>
<td>3.87</td>
<td>79</td>
<td></td>
</tr>
<tr>
<td>Parietal inferior</td>
<td>R</td>
<td>38</td>
<td>−46</td>
<td>48</td>
<td>3.83</td>
<td>26</td>
<td>40</td>
</tr>
<tr>
<td>Frontal operculum</td>
<td>L</td>
<td>−44</td>
<td>8</td>
<td>24</td>
<td>3.74</td>
<td>36</td>
<td>46</td>
</tr>
</tbody>
</table>
a negative one in the calcarine/lingual regions. The SMA, in turn, was activated by both neutral and beautiful stimuli similarly, though not by ugly. In turn, the mOFC, the posterior and middle parts of the cingulate, and the precuneus appeared activated by both ugly and beautiful stimuli comparably. The left angular and middle frontal gyri were more active to beautiful stimuli, though some degree of activation of these areas by ugly can be
alleged. Finally, the neutral differed noticeably from the other two esthetic categories in activating large portions of the somatosensory and motor systems bilaterally, including the cerebellum, together with parts of the anterior insula and the frontal operculum, again bilaterally, as well as small portions of the right inferior frontal gyrus and IOFC.

Before discussing in depth these results, a cautionary note is in place regarding the appropriateness of treating the esthetic dimension as a continuum and, then, the suitability of treating relationships as linear or non-linear. Esthetic categories were evaluated in the scanner as three relatively independent categories; however, this categorization was based upon the individual ratings of the presented stimuli, performed a few days before the scanning session and using a scale from 1 to 10 (from "very ugly" to "very beautiful"). In this regard, our procedures reliably reproduce those of most previous literature using fMRI in the esthetic domain (e.g., Kawabata and Zeki, 2004; Winston et al., 2007; Ishizu and Zeki, 2011), and this is mainly the result of technical constrains within the MRI environment. On the other hand, we cannot give it for granted that ugliness and beauty constitute two opposite extremes of one continuum, and indeed this study aimed at clarifying this point (this is again a common place in the literature). In fact, the use of a 1–10 scale for rating the stimuli does not necessarily entail that we assume any linear relationship; rather, it is a customary method for stimulus categorization and selection. Accordingly, treating our categories as related linearly (or not) might be considered as relatively inappropriate, though admissible and common in the frame of research on the neural basis of esthetics. It is actually a conventional approach to graphically describe differences and similarities in the magnitude of activation of a given neural region as a function of esthetic category.

Admitting these restraints, our results suggest that whereas certain areas seem to exhibit a linear relationship across esthetic judgments, supporting ugliness as the lowest extreme of a beauty continuum, or the highest extreme of an ugliness one, other brain regions were involved alike by both the very beautiful and the very ugly stimuli. Overall, our results imply that it is not extra specific activity within a brain region that is specialized for an particular type of esthetic category, either ugly or beautiful. That is, no area exhibited the highest activation for ugly stimuli that was similarly inactive, or less active, for both neutral and beautiful. The same applies to beauty. However, a de-activation, or at least a much lower activation of the SMA characterized ugliness; although this could be argued as some kind of specialization for an esthetic category, it would be so in negative terms –i.e., it is not a specific region for ugliness, as it was actually activated by neutral and beautiful stimuli equally. The difference between beauty and ugliness in the brain, as a minimum in relation to extreme samples of these categories from natural, biologically and socially relevant stimuli (faces and bodies), exhibits accordingly a complex picture by virtue of which one stimulus is categorized as ugly or beautiful depending on the constellation and the degree of brain activations and de-activations it evokes. Most involved regions were so in a manner that would support ugliness and beauty as linked, non-independent semantic categories within the human brain. Philosophical debates on this subject (e.g., Henderson, 1966; Bachmetjevas, 2007; McConnell, 1995).
should take this type of findings into consideration, a scenario otherwise resembling the case of other polarized semantic categories of the human brain, such as – e.g. – love and hatred (Zeki and Romaya, 2008).

A positive linear relationship for the dimension ugly-neutral-beautiful mainly involved NAcc and the ACC, which is line with a number of previous studies on beauty and attractiveness, including sexual attraction and desire (e.g., Vartanian and Goel, 2004; Winston et al., 2007; Cacioppo et al., 2008; Cloutier et al., 2008; Mende-Siedlecki et al., 2013; for an extensive review, see Brown et al., 2011). Typically, the NAcc is considered one of the main pleasure centers of the brain, systematically activated during the perception of pleasant and emotionally arousing stimuli (Sabatinelli et al., 2007). In this regard, this result would support the general assumption that beauty conveys highly positive emotions, while this would not be the case for ugliness. Even though, this is not a necessary conclusion given that the NAcc is also a crucial center for overall reward and reinforcement regardless of emotional valence (e.g., Rolls, 2007).

Indeed, one of the limitations of the present study is that emotional valence and activation of the stimuli were not explicitly scored – again, a situation common to most of the esthetics literature. Nevertheless, other regions related with rewarding processes, such as the mOFC, were equally activated by both the very ugly and the very beautiful stimuli (see below). Consequently, it is our interpretation that the activation of the NAcc is most probably reflecting pleasure processes linked to the contemplation of very beautiful persons. The role of the ACC in turn is certainly more complex, as it has been related to a number of processes other than pleasure or esthetic judgements of beauty, such as cognitive conflict (Mitchell, 2006), response planning and selection (Stevens et al., 2011), or pain (Vogt, 2005). Indeed, in the Kawabata and Zeki (2004) study, although the activity in the ACC was maximal for beautiful stimuli, it did not exhibit a linear relationship with beauty, appearing more activated for ugly than for neutral stimuli. Accordingly, the relationship of the ACC to judgements of beauty may not be as straightforward as it appears the case for the NAcc. Further, it seems also possible that the particular pattern of activations of the ACC observed in our data relates to some kind of interaction between esthetic judgements and self-referential and self-related processes presumably also involved in our task (see the Introduction and below); the ACC is actually part of the medial cortical structures involved in the latter processes (Pöppel et al., 2013; Lutz et al., 2013).

In turn, a negative relationship for the ugly-neutral-beautiful dimension was mainly found in the calcarine/lingual regions. Both regions are primary portions of the visual system (e.g., Mendoza and Foundas, 2008); in addition, the lingual gyrus is very well-connected with limbic regions (Isenberg et al., 1999) and is usually involved in the processing of complex images (Mechelli et al., 2000), selective attention (Mangun et al., 1998), and even in the attribution of intentions to others (Brunet et al., 2000). Our result harmonizes well with previous reports of these regions being more activated for negative pictures (Mitchell et al., 2006; Fusar-Poli et al., 2009), and is somehow in line with Ishizu and Zeki (2011) who found a linear activation with ugliness in inferior occipital and fusiform gyri. However, other studies have reported a relationship with esthetic judgements opposite to ours involving occipito-temporal and lateral occipital regions (Di Dio and Galese, 2005; Vessel et al., 2012). Overall, it seems that visual areas are indeed especially involved in esthetic judgements of visual stimuli (see also Chatterjee, 2014), though the sign of this relationship might exhibit different values probably as a function of task demands and contextual circumstances.

On the other hand, a number of regions displayed comparable or closely similar activation for either extreme esthetic category. The main regions in this regard comprised the precuneus and the middle and posterior cingulate cortices, as well the mOFC. The activation of the mOFC by extremely ugly stimuli will be discussed apart. The relatively equivalent activation by ugly and beautiful stimuli of the medial parietal regions might appear as relatively unexpected, given previous studies in which these regions were actually related to judgments of beauty (e.g., O’Doherty et al., 2003; Cloutier et al., 2008). Even though, precuneus and posterior and middle cingulate regions conform to a relatively unitary functional brain area involved in a number of higher-order cognitive processes, representing a major hub within the DMN activated during resting conscious states (Buckner et al., 2008). Among the functions ascribed to the DMN, and particularly to this posterior medial parietal hub, are included the representation of the self, or self-consciousness, as when one rates own personality compared to those of other people (Lou et al., 2004). As mentioned in the Introduction, other functions of the DMN comprise empathy, theory of mind, and self/other distinction. Overall, the posterior cingulate and the precuneus compose a discrete functional unit crucial for conscious information processing (Vogt and Laureys, 2005). Given these overall functional features of the precuneus and the middle and posterior cingulate cortices it appears to us hard to credit them as specifically related to esthetic judgements of beauty; its activation by both extremely ugly and extremely beautiful stimuli could rather be interpreted in terms of the personal relevance of those stimuli in relation to oneself (also in line with Vessel et al., 2012 for esthetic judgement in general), and consistent with the type of stimuli used in the present study.

The involvement of the DMN in esthetic judgements has been stressed recently by several authors (e.g., Vessel et al., 2012; Cela-Conde et al., 2013; Vartanian and Skov, 2014). In line with this, as well as with our discussion above, we found an involvement of the left angular gyrus, which is also a critical portion of the DMN (Buckner et al., 2008). The latter was more activated by beautiful stimuli, though some degree of activation by ugly in comparison to neutral stimuli could also be alleged. Interestingly, Kawabata and Zeki (2004) reported an activation in the parietal regions compatible with left angular gyrus and also exhibiting this same type of non-linear relationship with esthetic categories. On the other hand,
the left middle frontal gyrus was likewise more activated by beautiful stimuli and exhibited a non-linear pattern in relation to esthetics somehow resembling those of the precuneus, middle and posterior cingulate, and the angular gyrus. Although this region does not properly pertain to the DMN (Buckner et al., 2008), it belongs to the dorsolateral prefrontal cortex (dlPFC), which, paralleling the DMN, is involved in task-relevant and decision-making judgements, including esthetic decisions regardless of their actual category (Ishizu and Zeki, 2013). Overall, several circuits involved in decision-making were significantly involved in our study and resulted in more activation by esthetically extreme stimuli, particularly by the beautiful ones. A large portion of these circuits belong to the DMN and seemingly relate with self-referential and self-related information processing, located in the medial cortical regions normally related with these types of processes (Pöppel et al., 2013).

This line of argumentation can also be used to understand the significant activation of the mOFC by the very ugly stimuli, comparable in intensity to the very beautiful ones. Traditionally, the mOFC is considered a reward-processing region (O’Doherty et al., 2001), and has been consistently —though not at all times— related with judgments of beauty (e.g., O’Doherty et al., 2003; Kawabata and Zeki, 2004; Di Dio et al., 2007; Winston et al., 2007; Kirk et al., 2009a,b; Liang et al., 2010; see also the reviews by Brown et al., 2011, and Mendes-Siedlecki et al., 2013). To this regard, it has recently been proposed as the very main center for beauty in the brain (Ishizu and Zeki, 2011). Consistent with this, we found a significant activation of the mOFC by the very beautiful stimuli; but contrary to this, we found the same for the very ugly. Findings pertaining to the OFC, including its medial part, are not entirely homogenous in the literature, nevertheless. Overall, a consensus exists that whereas the mOFC is activated by rewards, the IOFC is so by punishments (O’Doherty et al., 2001). Even though, some studies have reported the activation of the mOFC by negative experiences such as mental fatigue (Tajima et al., 2010) or aversive goals (Plässman et al., 2010). Further, in the studies by Cloutier et al. (2008) and Winston et al. (2007) on facial attractiveness, activations of the mOFC only emerged for male participants, not for female, even if both genders valued beautiful stimuli. Accordingly, the straightforward identification of beauty with mOFC might be somehow misleading, its activation rather depending on a plethora of factors, such as subjective utility, task demands, and many others (more arguments on this can be found in Minissale, 2013, pp. 81–83).

In our opinion, the activation of the mOFC by very ugly stimuli in the present experiment is largely related with the specific demands of our task and the interpretation of this region not as a ‘beauty’ center, but as related to reward (O’Doherty et al., 2001), value, and preferences (Schultz et al., 2000; Schoenbaum et al., 2011). This appears to be the case, particularly considering that the stimuli had been individually selected by each participant prior to the scanning session. This interpretation would complement with the fact that the mOFC also participates in self-perception and self-regulation in social cognition (Flagan and Beer, 2013), and indeed is part of the medial cortical structures involved in self-referential and self-related processes (Northoff et al., 2006; Pöppel et al., 2013). Further, this interpretation harmonizes well with our activations of portions of the DMN for both beautiful and ugly stimuli comparably (see above). Indeed, it seems that the substantially social value of our stimuli, consisting in bodies and faces of people of either gender, with which one could compare oneself in order to achieve an esthetic judgment – i.e., this is not a study on ‘attractiveness’ –, might elucidate most of the particularities of our findings. This comprises the activation of large mOFC by very ugly stimuli, as well as the overall strong implication of both anterior and posterior medial cortical areas by either type of extreme esthetic category.

The neutral stimuli noticeably differed from the other two esthetic categories in activating portions of the somatosensory and somatomotor systems bilaterally, together with parts of the anterior insula and the frontal operculum, again bilaterally, as well as small portions of the right inferior frontal gyrus and IOFC. This was supplemented by notably longer reaction times and higher error rates, most probably indicating that our participants experienced the highest levels of difficulty when classifying stimuli as neutral, and might actually reflect the difficulty of the hyper-social human brain to categorize someone as truly indifferent. In our view, these strong activations indeed relate to the difficulty of the task. However, the fact that they were mostly bilateral (including the cerebellum), and some of them even preferentially right, would imply that it is not the difficulty in assigning a motor response for the required rating task what activated these regions into the scanner, where our right-handed subjects had to respond with the right hand. Instead, it appears to us that this activity might be actually reflecting evaluation processes of the stimuli based on overall touch and somatosensation, that is, on the implication of the whole somatosensory and somatomotor systems in this endeavour. The body is indeed a ‘corpo-real connoisseur’ (e.g., Radman, 2013). Hence, the representation of the proper body and face in the cerebral cortex could be used as main processors to esthetically evaluate the bodies and faces of others. This line of argumentation coalesces with most recent theories of embodied cognition (e.g., Barsalou, 2008; Carota et al., 2012). What is more, the involvement of the anterior insula and opercular portions, bilaterally, would also be in this line, as these regions also relate to proper body sensations, in this case to visceral and interoceptive awareness of body states (e.g., Brown et al., 2011). The assumption that neural stimuli were hard to classify probably explains why the IOFC, typically related with punishment (O’Doherty et al., 2001), was also involved here.

Overall, the results obtained for neutral stimuli appear of the highest interest, as they reveal clues on how the human brain evaluates the physical value of others. However, they also advice for some caution on our conception and use of this category in the present study. The neutral appeared much more heterogeneous and inconsistent than the other two esthetic categories,
which would add to the limitations outlined above on linear and non-linear relationships among categories. This limitation, however, appears inherent and unavoidable for these type of studies.

The activations of the SMA by neutral stimuli should be excluded from the explanations above, even if it is a significant portion of the cortical motor system, mainly because it was comparably activated by both neutral and beautiful stimuli, while it was non-activated, or significantly less activated, by ugly. As an explanation for this, and considering the involvement of SMA in planning, anticipating, and imitating behavior of others (e.g., Fincham et al., 2002; Manthey et al., 2003; Iseki et al., 2008), as well as in social cognition and empathy (Eslinger et al., 2011), we speculate that the motor plans and imagined actions one could normally formulate in relation to a person in front seem revoked when that person is very ugly.

In sum, from the neurosciences it seems that common neural circuits are largely, if not totally, shared by both beauty and ugliness, paralleling proposals for other pairs of otherwise entirely opposed semantic categories, such as love and hatred (Zeki and Romaya, 2008). It seems that both esthetic judgements are the result of both equivalent neural circuits are largely, if not totally, shared by both significant samples of either both esthetic extremes, of otherwise entirely opposed semantic categories, such as beauty and ugliness, paralleling proposals for other pairs

Acknowledgments—This research was supported by grant PSI2010-19619 from the Ministerio de Economía y Competitividad (MINECO, Spain). M. Urrutia is supported by the Neurocog Project (ACIISI, Canary Islands and ERDF, European Union). The authors wish to thank Eva Manzanedo and Francisco Muñoz for their help in data analyses.

REFERENCES


