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Electrophysiological brain dynamics during the esthetic judgment of human bodies and faces

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ABSTRACT

This experiment investigated how the esthetic judgment of human body and face modulates cognitive and affective processes. We hypothesized that judgments on ugliness and beauty would elicit separable event-related brain potentials (ERP) patterns, depending on the esthetic value of body and faces in both genders. In a pretest session, participants evaluated images in a range from very ugly to very beautiful, what generated three sets of beautiful, ugly and neutral faces and bodies. In the recording session, they performed a task consisting in a beautiful–neutral–ugly judgment. Cognitive and affective effects were observed on a differential pattern of ERP components (P200, P300 and LPC). Main findings revealed a P200 amplitude increase to ugly images, probably the result of a negativity bias in attentional processes. A P300 increase was found mostly to beautiful images, particularly to female bodies, consistent with the salience of these stimuli, particularly for stimulus categorization. LPC appeared significantly larger to both ugly and beautiful images, probably reflecting later, decision processes linked to keeping information in working memory. This finding was especially remarkable for ugly male faces. Our findings are discussed on the ground of evolutionary and adaptive value of esthetics in person evaluation.

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1. Introduction

The ability to appreciate esthetics in our environment is intrinsic to the human cognition (Chatterjee, 2014). In the last decade, research on neuroesthetics has prided increasing evidence on the neural correlates of visual esthetic experience (i.e., appreciation, apprehension, judgement, etc.) in a heterogeneous variety of objects (Cela-Conde et al., 2013, 2004; Kawabata and Zeki, 2004; Vartanian and Goel, 2004; Jacobsen et al., 2006; Cupchick et al., 2009; Munar et al., 2012). This research has been grounded on cognitive models of the esthetic experience. For instance, Leder et al. (2004) proposed a comprehensive model of esthetic appreciation and judgment, which includes five stages: perceptual analysis,

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implicit memory integration, explicit classification, cognitive mastering and evaluation. This model proposes that both cognitive mastering and evaluation stages are the source of the esthetic preference, linked to the esthetic judgment. The question here is, to what extend such cognitive processes underlying esthetic experience are common to the great variety of perceptual objects (Brown et al., 2011). Still further, to what extend different esthetic categories (beautiful or ugly) deserve different cognitive processes.

Likely answers to these questions could be explored evaluating brain-based available models on esthetics. For instance, Chatterjee (2003) advised that esthetic preference involves three processing stages, common to the perception of any visual stimulus. Early visual processes take place at low level in the visual stream; an intermediate level relates to the formation of a coherent perceptual representation; and at a later level, multimodal processing allows recognizing and associating with stored meanings. Corresponding neural sources underlying these processes are placed in occipito-temporal cortices in the ventral visual stream (Pessoa et al., 2003). Chatterjee (2003) also suggested that other non-visual processes are involved in the decision-making processes that can enhance the processing of visual attributes, with intervention of fronto-parietal cortices.

Other contributing factors in the esthetic experience rely on affective and motivation components. Esthetic images can be conceived to convey an intrinsic global affect value based on hedonic tone between a positivity and a negativity activation dimension that represents subjective components of implicit behavioral approach or withdrawal, respectively (Watson et al., 1999). However, Markovic (2012) points out that the esthetic experience emerges beyond the perceptual properties of the object, eliciting the higher level of esthetic feelings of pleasure (see also Kubovy, 1999; Martindale and Moore, 1988; Winkielman and Cacioppo, 2001). In his view, beauty must transcend from its extrinsic (feature-based, say a beautiful object) to its intrinsic (symbolic-based, say the object of beauty) value. According to this, even ugly objects can elicit an esthetically aroused experience due to its oddity (e.g., esthetic fascination with deformation, monstrous, grotesque, morbid, horrible, and other kinds of ugliness; Eco, 2007; Furnham and Avison, 1997; Rawlings, 2003; Silvia, 2009). A number of studies have also posited that esthetic preference of visual stimuli involves different levels of affective valence and motivational instances. Beauty and preference ratings correlate with positive affective states, what leads to the assessment of the reward value of the stimuli (Kawabata and Zeki, 2004) and the integration of such rewarding information with cognitive processing, configuring the appropriate response selection (Vartanian and Goel, 2004).

Another crucial factor related to pleasure or fascination (and conversely, to displeasure or fright) of the esthetic experience is arousal. Some behavioral studies suggest that the greater the arousal, the greater the esthetic fascination (e.g., Marcovik, 2012). Although much is known regarding beautiful material in this regard, less attention has been devoted to evaluate esthetic response to ugly high-arousing material. In this sense, the model proposed by Berlyne (1974) puts together arousal, preference, and collative variables (complexity, uncertainty, novelty, ambiguity, etc.), so that salient, complex, irregular, and unusual stimuli have greater arousing potential. Related to esthetics, beautiful and ugly stimuli may entail high motivation to attend and evaluate their features. Moreover, they may be experienced as more rewarding, appetitive and attractive (or avoidable and repulsive) than simple, regular, and ordinary stimuli (Raymond and Narayanan, 2009).

Undoubtedly, the human body and face incorporate perceptual features able to elicit an intense esthetic experience, assuming its biological meaning. Darwinian approaches to the study of facial attractiveness posit that the features of beautiful faces (and by extension, the body) convey important biological signals of mate value that motivate behavior in others (Etcoff, 1999; Grammer and Thornhill, 1994; Perrett et al., 1998; Symons, 1995). It is important to note that in most contemporary cultures, we do not get to see many nude bodies as compared to faces, so we probably do not form the same kind of prototypes of averaged bodies. This fact may have some influence on attractiveness. Even in the case that faces and bodies were both attractive, we may ask whether we assign more value to one than the other. Until now, these assumptions have not been addressed by neuroesthetics, which contrasts with the powerful biological and adaptive value of the body (reproductive potential, mating and fertility).

1.1. *Cognitive neuroscience of the experience of beauty and ugliness*

While evolutionary psychology is interested in the 'why' of esthetics, cognitive neuroscience is interested in the 'how' of esthetics. A main question to be addressed by researches on neuroesthetics is whether similar or distinct brain areas are devoted to process the experience of beauty and of ugliness. In this line, an fMRI study by Kawabata and Zeki (2004) proposed that beauty and ugliness constitute polar extremes of a continuum. They presented to the subjects with different categories of objects (portrait, landscape, still life, or abstract composition) and observed that the neural processing of categories is correlated with the activation of distinct and specialized visual cortical areas. They also found that neural activity was greater in the medial orbito-frontal (mOF) cortex for stimuli classified as beautiful, as well as in the motor cortex for stimuli classified as ugly. This study, and others (Ishizu and Zeki, 2013; 2011; Chatterjee, 2010) using fMRI conclude that there are no specific neural networks dedicated to esthetics. Instead, they exist distributed brain areas dedicated to perceptual processing of esthetic objects, and some others (non-perceptive areas) dedicated to take semantic decisions on the object depending on the task requirements (esthetic judgments or evaluative of interestingness, for instance). In this line, a recent study by Martín-Loeches et al. (2014) found that activations of the mOFC can also be found for ugly stimuli when they are faces or bodies of persons, and that the motor cortex was noticeably most activated by neutral, not ugly stimuli. Therefore, key questions to be addressed would be, which, how, and when brain networks are interplaying in the esthetic judgement on the basis of the visual attributes of the objects.

On the one hand, the activity of a wide-distributed neural network related to evaluative judgment of esthetically pleasing visual stimuli has been associated with the lateral and medial prefrontal cortex (Cela-Conde et al., 2004; Cupchick et al., 2009; Jacobsen et al., 2006). Particularly, medial orbitofrontal cortex has a critical role to the representation of reward value, pertaining as well to a network involved in self-other person evaluations, this probably explaining why activations of the mOFC can also be observed for stimuli of ugly persons (Martín-Loeches et al., 2014). The anterior cingulate is also involved in our sense of self (Blood et al., 1999; Blood and Zatorre, 2001; Cupchick et al., 2009; Kawabata and Zeki, 2004), but its involvement in esthetic judgment of beauty appears more complex, as it is also activated a variety of situations, such as cognitive conflict (Mitchell et al., 2006), response planning and selection (Stevens et al., 2011), or pain (Vogt, 2005). On the other hand, little evidence has been devoted to the judgment of esthetically ugly stimuli in this sense. As mentioned previously, the fMRI study by Kawabata and Zeki (2004) yielded more activation in the motor cortex to ugly pictures, which was interpreted as a likely motor pre-activation of withdrawal. Moreover, it is well known that amygdala is a key structure involved in the preference for visual aversive stimuli (Adolphs and Tranel, 1999), and expected to be activated in studies of esthetic appreciation of negative stimuli. Winston et al. (2007), however, showed that activity of amygdala followed a non-linear response pattern in relation to attractiveness (particularly in faces). In other words, both attractive and unattractive faces elicited the highest activation of the amygdala compared to intermediate attractive faces. Further, in the study by Martín-Loeches et al. (2014), the amygdala did not appear involved in esthetic judgements of faces and bodies.

Although some effort has been done, studies on neuroesthetics of the human body as a whole have been less addressed. For instance, Calvo-Merino et al. (2010) and Cross et al. (2011) have studied the neural correlates of perceiving and evaluating the beauty of body dancing, what involves a complex neural network comprising associative occipito-temporo-parietal regions, and premotor cortices. Both studies converge in the fact that, when bodies are involved, beauty appreciation is inherently sensorimotor in nature. More effort must be done with regard to static body, however, putting the focus on the esthetics of its intrinsic features. In the study by Martín-Loeches et al. (2014) nude bodies were included in the stimuli, though the corresponding results did not yield significant differences with those obtained for faces. Further research is granted to better establish whether faces and bodies may be differently processed during esthetic judgement, as they presumably diverge in biological and adaptive value.

To summarize, the sequence of information processing of esthetic visual pleasing (and unpleasing) faces and bodies, starts in primary–secondary visual networks. Then, this information is presumably processed in different and specialised occipital areas (extrastriate body and faces areas, EBA and FFA, respectively), which interplay with the reward system. The more a stimulus is liked, the more the reward system becomes activated. Meanwhile, as beautiful and ugly stimuli engage the observer and capture his/her attention and responds to them making evaluative judgments, the parietal and frontal cortical regions would become presumably involved (Schweinberger and Burton, 2003; Haxby et al., 2000; Kanwisher, 2000; Slaughter et al., 2004; Downing et al., 2004; Martín-Loeches et al., 2014). The sequential order of such cognitive and affective processing can be better addressed by ERPs approaches.

1.2. *Electrophysiological correlates of esthetics focused on the human body*

In the temporal domain, an event-related potential approach enables to better understand the brain dynamics underlying the esthetic experience, from the lower (perceptual) to the higher (evaluation and judgment) stages. Correspondingly, the time course and topography of visual ERPs are modulated by the content of the ongoing stimulus, taking into account the level of elaboration in the processing stream (Delplanque et al., 2004).

Jacobsen and Höfel (2003) provided a general ERP-based view of cognitive processes involved in esthetic appreciation. In that study, they observed that perceptual (symmetric vs non-symmetric judgement) and esthetic (beautiful vs ugly judgment) tasks engaged different brainwaves patterns at early and late latencies. On the one hand, both symmetry and beauty judgments involved posterior ERP modulations that were associated with stimuli elaboration and integration. On the other hand, only esthetic judgments engaged a two-stage process: (1) an early negativity in the 300–400 ms interval, related to an impression formation, and (2) a late positivity in the 440–880 ms interval, related to an evaluative esthetic-specific categorization. The authors concluded that the categorization of the esthetic properties of geometrical shapes seems to induce a higher level of attention, but particularly the recognition of beautiful stimuli elicited the highest level of arousal. In summary, an initial impression may occur in the first 300 ms; between 300–600 ms a deeper esthetic evaluation apparently takes place; and finally, later than 600 ms, long lasting esthetics processing (evaluation, memory, etc.) may occur.

Further lines of evidence derive from Wang et al. (2012). They observed that the P200 amplitude was greater to less beautiful adornments than to the beautiful ones, suggesting that early assessment of arousal is taking place, particularly for negative stimulation. This ERP effect could be related to an early attention-bias to negative valence material. At later latencies, a P300 component and a late positive complex (LPC) have been classically described as indices of task difficulty (Katayama and Polich, 1996; Picton, 1992), stimulus classification mechanisms (Kutas et al., 1977; McCarthy and Donchin, 1981), and its amplitude reflecting the amount of attention resources allocated (Humphrey and Kramer, 1994). Although both P300/LPC components usually emerge together, the P300 appears to be transient and followed by the LPC, the latter exhibiting longer duration and different topography (fronto-central and parietal sites, respectively). Cuthbert et al. (2000) proposed that P300 and LPC are functionally related as they appear enhanced to motivationally relevant stimuli. However, LPC seems to index high-level allocation of attention resources, semantic categorization (esthetic preference for instance), and the representation of stimuli in working memory (Cuthbert et al., 2000; Codispoti et al., 2007; Azizian and Polich, 2007).

Concerning face stimulation, P200 and LPC may be modulated by the degree of attractiveness (Werheid et al., 2007;

Chen et al., 2012), as well as they may be enhanced for pleasant and unpleasant, compared to neutral stimuli (Hajcak et al., 2009; Foti et al., 2009; Schupp et al., 2004). Hence, P200 and LPC have been related to attractiveness discrimination (Chen et al., 2012), affective evaluation processes, detection of the motivational relevance of the stimulus (Cunningham et al., 2005), dynamic allocation of attention (Hajcak et al., 2009; Ferrari et al., 2008) and memory encoding (Dolcos and Cabeza, 2002).

Together, these ERPs studies reveal that esthetic experience entails early brain activity associated with evaluative processes representing a first impression formation which influences ongoing high-level processes related with attention, perception, response selection and judgement. However, ERP literature also reveals large heterogeneity in methodological approaches, both in esthetic judgements (attractiveness, pleasantness, beautifulness, etc.) and in esthetic objects. In such diversity esthetics of human faces are represented but no so much the rest of the body. To fill these gaps, in this study we presented the participants with faces and bodies, differing in subjective esthetic value (beautiful, ugly, neutral). Based on the above reviewed literature, we hypothesize that:

a) Automatic attention is differentially engaged in the formation of an early esthetic impression based on perceptual and affective properties. Following the suggestion of an early attention-bias to negative valence material, we expect early ERP modulations to be larger in amplitude to ugly than beautiful stimuli.
b) Processes of evaluation and categorization of esthetic stimuli differentiate esthetic content, depending on the amount of attentional resources delivered in its short-term representation. We expect P300 component modulations as a function of the motivational value of stimuli based on respective biological meaning of the beautiful and ugly images.
c) Assuming their different biological meaning, esthetic processing can be distinguished between faces and bodies, as well as between male and female. We expect different ERP profiles to beautiful and ugly stimuli, as a function of the part of the body and gender.

Finally, although limitations exist due to conspicuous technological and methodological dissimilarities, indirect comparisons will be made when possible between the present data with ERPs and those by Martín-Loeches et al. (2014) with fMRI using the same stimuli and procedures as here.

2. Results

2.1. Behavioral

Performance: Accuracy, or concordance with prior individual ratings, was higher to both beautiful and ugly images than to neutral images (Table 1). Such difference was statistically significant ($F_{2,\,38}=12.4$; $p<0.001$, beautiful vs neutral, $\Delta=5.6$; $p=0.01$, and ugly vs neutral $\Delta=6.7$; $p<0.001$). No statistic significance was obtained comparing accuracy to beautiful vs ugly stimuli.

Table 1 – Results of performance.

Body Part	Gender	Beautiful	Neutral	Ugly
Face	*Male*	86.2	65	88.7
	Female	87.8	63.4	87.8
Body	*Male*	85.9	68.4	89.7
	Female	83.7	62.2	90.9

2.2. ERP results

A visual inspection of the grand averages to each esthetic target stimulus reveals three main ERP waveforms effects at early, middle and late latencies (Fig. 2(A)). At short latencies, a P200 component was elicited larger to ugly stimuli than beauty at central sites. At middle latencies a positive-going waveform (P300) emerged, that was larger to beautiful stimuli and elicited at fronto-central sites. Finally, at late latencies, esthetic stimuli elicited larger LPC amplitude with respect to neutral stimuli at parietal and slightly left sites. A slightly higher LPC amplitude to ugly than to beauty stimuli can observed.

In order to determine latency windows to compute ERPs mean amplitudes, we subtracted the waveforms from beautiful and ugly stimuli to that of the neutral stimuli (Fig. 2(B)). Accordingly, the corresponding time windows were, P200: 200–240 ms, P300: 280–420 ms and LPC: 500–700 ms. We dissociated P300 component from the LPC by two reasons. First, the component elicits different ERP effects to beautiful and ugly images; second, the topography was different than that of LPC (Fig. 2(C)). The repeated-measures ANOVA yielded significant main effects for esthetics in each of the three selected time windows (Table 2). No other main effect was observed. Post-hoc pairwise comparisons revealed that the amplitude of P200 component was increased in the ugly stimuli compared to both beautiful and neutral stimuli ($\Delta=0.61\,\mu V$; $p=0.03$ and $\Delta=0.84\,\mu V$; $p=0.02$, respectively). The amplitude of P200 was not statistically different between beautiful and neutral stimuli. Regarding P300 component, beautiful stimuli showed an increased amplitude compared to both ugly and neutral stimuli ($\Delta=1.0\,\mu V$; $p=0.001$ and $\Delta=1.2\,\mu V$; $p<0.001$, respectively). The amplitude of P300 was not statistically different between ugly and neutral material. Finally, regarding LPC, both beautiful and ugly stimuli showed an increased amplitude compared to neutral stimuli ($\Delta=1.1\,\mu V$; $p=0.004$ and $\Delta=1.5\,\mu V$; $p=0.001$, respectively). The amplitude of LPC was not statistically different between beautiful and ugly stimuli.

Furthermore, interactions of esthetics by body part as well as the triple interaction esthetics by body part by image gender appeared significant concerning the P300 component (Table 2).These interactions revealed (Fig. 3) that the largest P300 amplitude was obtained for female bodies, whereas the lowest one corresponded to male bodies; furthermore, ugly female bodies and—to a lesser degree—male faces also appeared to exhibit some degree of P300 activity.

Finally, due to statistical power limitations, analyses splitting the sample as a function of participant's gender were considered unsuitable despite its potential interest. Our results would apply, therefore, to general principles of person esthetic evaluation irrespective of the gender of the viewer.

Fig. 1 – Depiction of the experimental paradigm. It shows an example of a block consisting on beauty male faces intermixed with one ugly and a neutral image. Each image was preceded by a cross-fixation to prevent eye movements during image presentation.

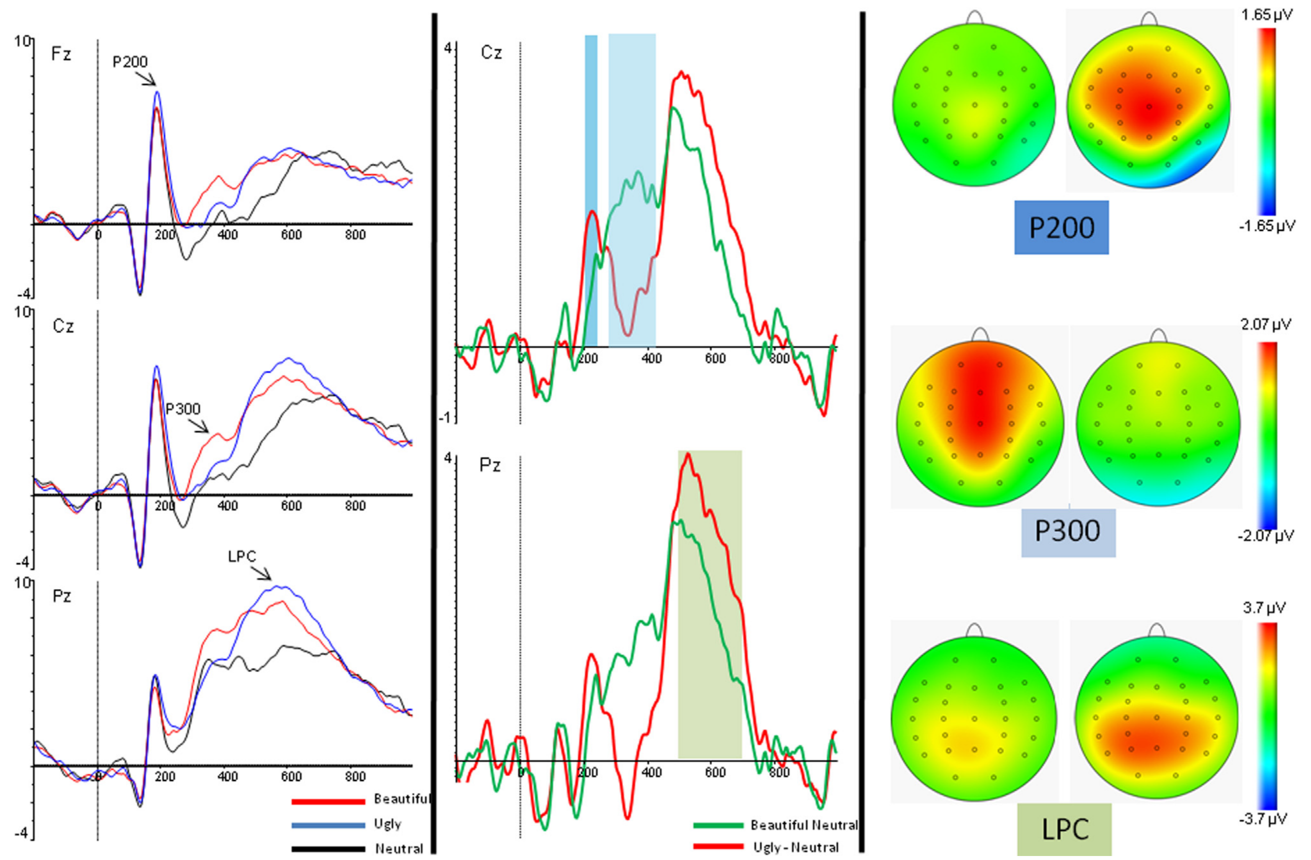

Fig. 2 – (A) Averaged ERPs for the beauty, ugly and neutral conditions. (B) Difference waves of beauty minus neutral and ugly minus neutral. (C) Topographical maps of the main ERPs components at their respective time windows.

Table 2 – ANOVA main results.

Factors/time windows (*d.f.*)	200–240 ms	280–420 ms	500–700 ms
Esthetics (*d.f.* = 2.36)	7.7**	15.7***	11.8***
Esthetics × electrode (*d.f.* = 52.936)	4.4***	5.3***	9.1***
Esthetics × body part (*d.f.* = 2.36)	2.8†	3.5*	n.s.
Esthetics × body part × gender (*d.f.* = 2.36)	n.s.	5.7**	n.s.

* $p<0.05$.
** $p<0.01$.
*** $p<0.001$.
† $p<0.1$.

3. Discussion

In this study, we were interested in investigating whether visuo-perceptual processing of faces and bodies, multimodal integration and decision-making processes are differentially interlinked in a beautiful–ugly judgement task. Assuming that face and body of male and female have intrinsic and different biological meanings, we expected that their respective esthetic processing would be dissociated.

Overall, this study reveals that judgment on esthetics of the human face and body mobilizes different attentional resources

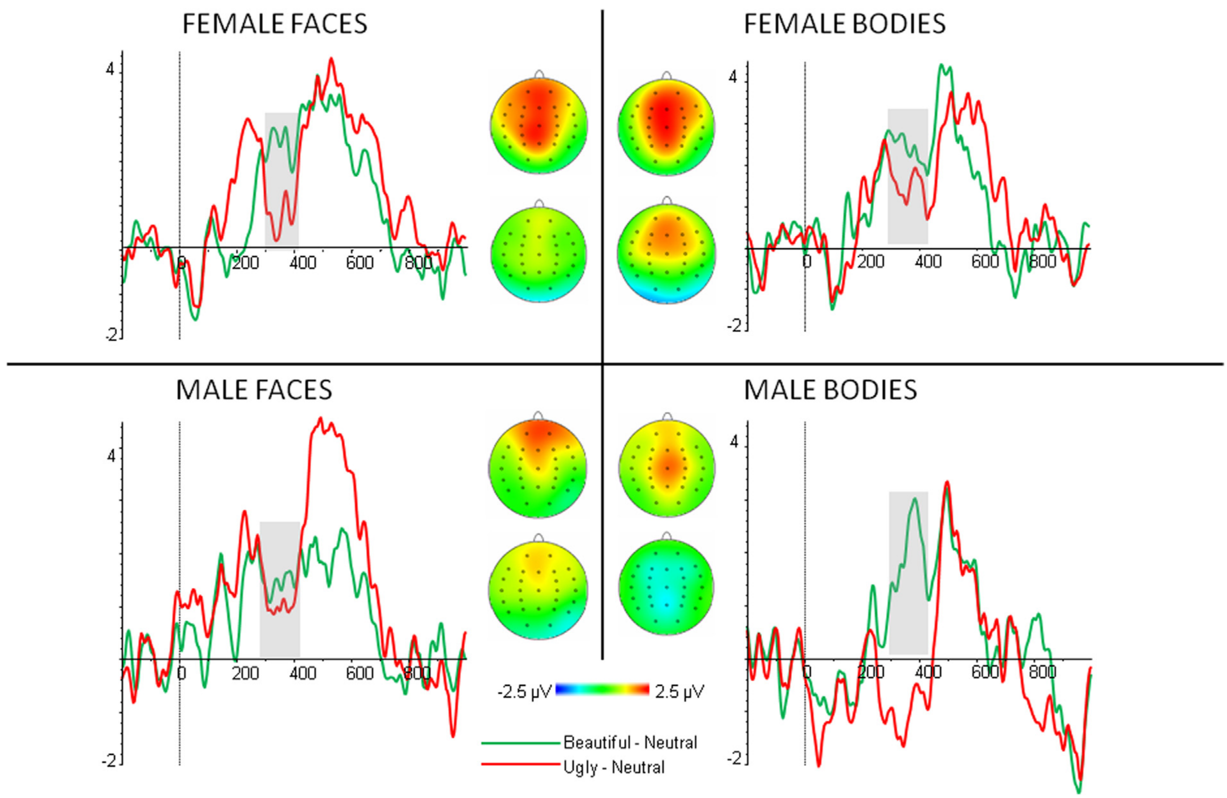

Fig. 3 – ERP difference waves relative to the triple interaction esthetic by body part by image gender. In each part, the P300 component is displayed at Cz. Next to each ERP, topographies of the difference waves beautiful minus neutral (at the top), and ugly minus neutral (at the bottom) are displayed in the P300 time window.

throughout the processing of beautiful and ugly images. This implies that low-level processing of emotionally-neutral faces and bodies is modulated during a task of beautiful–ugly evaluation. High-level processing is further biased by the esthetic value when categorizing and decision-making take place. Integrative processing of esthetic content stimuli appears to be shaped by motivational and arousing properties of the images.

3.1. *Ugliness and the negativity bias effect*

Focusing on esthetic manipulation, ugly images elicited higher positive amplitude at relative early latencies (P200, 200–240 ms) compared to neutral images. This finding was specific to ugly material, as P200 amplitude to beautiful and neutral stimuli appeared similar. The P200 component has been linked to early attention according to affective features of the stimuli to be attended (Sergei et al., 2000). According to Wang et al. (2012), the early evaluation of less beautiful images engages an early attention-bias for such kind of material compared to beautiful material. They also suggested that negative material is early assessed based on the level of arousal, and our ugly stimuli were selected as being the ugliest assessed by the participants, making this material of great saliency and arousal. Other studies, like Smith et al. (2003) found an even earlier P100 effect using positive and negative material (selected from the International Affective Picture System), showing this component more amplitude to negative stimuli. It seems clear that the faster the cognitive system differentiates positive and negative stimuli, the faster it engages an adaptive response to biological relevant stimuli. Though no explicitly emotional, our ugly, high-aroused material, may afford some negative evaluation to mobilize more attentional resources in its initial processing. In a similar vein, but using emotional stimulation, Carretié et al. (2001) observed a higher P200 in response to negative stimuli (different kinds of beetles) than in response to positive stimuli (nude models). They concluded that negative events may elicit larger attentional resources than positive events, supporting a negativity bias of attention to negative stimuli.

Accordingly, we could assume an affective component in esthetics from the very early processing stages (Cela-Conde et al., 2004; Jacobsen et al., 2006; Kawabata and Zeki, 2004; Vartanian and Goel, 2004). Moreover, we also could assume an intrinsic effect of “negativity bias” (Rozin and Royzman, 2001 for a review) in the attentional processes that may account for the increment in the P200 amplitude in our ugly images. This negativity bias operates automatically at the evaluative-categorization stage that in turn drives esthetic judgement of beautiful and ugly images (Cacioppo et al., 1997). Thus, we can conclude that ugly images used in our study could also be considered as negative stimuli to explain a likely attention bias effect. Further, and interestingly, this result seems to fully parallel activations in calcarine/lingual gyrus specifically for ugly stimuli reported by Martín-Loeches et al. (2014). Consistent with our arguments, these regions have been seen involved in selective attention (Mangun et al., 1998) and appear more activated for negative pictures (Fusar-Poli et al., 2009; Mitchell et al., 2006).

3.2. Encoding, evaluation and categorization processes

Other relevant findings related with later evaluative and decision-making processes, as revealed by P300/LPC components (Katayama and Polich, 1996; Picton, 1992; Humphrey and Kramer, 1994). It is noteworthy that P300 and LPC seem to show dissociated effects regarding the esthetic value. Beautiful material elicits larger P300 amplitude relative to ugly and neutral material. This effect was, for the most part, specific to beautiful material. In contrast, LPC amplitude was larger to both ugly and beautiful material compared to neutral stimuli.

The P300 component may be reflecting task-related categorization, as well as higher-order processes demanding attentional resources for evaluating and categorizing stimuli (Polich and Kok, 1995; Polich, 2007). Results show an increment in amplitude of this component to beautiful compared to neutral stimuli. The fact that P300 amplitude was particularly conspicuous to beautiful as compared to ugly and neutral stimuli probably suggests that beautiful images mobilized more attentional resources during esthetic evaluation and categorization processes. P300 modulations were also observed in many studies that used esthetics stimuli (faces) and attractive vs. unattractive judgment (Zhang and Deng, 2012; Johnston and Oliver-Rodriguez, 1997; Oliver-Rodriguez et al., 1999; Schacht et al., 2008). Particularly, Zhang and Deng (2012) observed an increase in P300 amplitude (P3b, 330–500 ms) to attractive stimuli. Comparable results were obtained by Oliver-Rodriguez et al. (1999). In this case, they used an oddball paradigm to test whether the classical P300 can reflect affective evaluation of stimuli ranging in attractiveness. They concluded that P300 processes appeared sensitive to the significance of events that would drive an individual to adaptively store and update contextual information. It is supposed that the core of such significance may be related to attentive, affective and sexual components, both derived from the perception of the face and body (Perrett et al., 1998; Downing et al., 2004). In our task, though esthetic judgment is not driven explicitly by emotional cues, we may assume that beautiful stimuli may activate brain areas dedicated to reward processing, as long as attractive stimuli have stronger motivational significance. In the end, reward and motivation impact on allocating more attentional resources during evaluation and categorization of beautiful (attractive) stimuli.

Evolutionary salient objects inherently engage attentional resources to represent them in high-order posterior associative cortex, this leading to strongly activate the appetitive or aversive motivational systems and corresponding behavioral patterns (Cuthbert et al., 2000). According to the differential results in P300 amplitude as reflected in gender by body part interactions, it seems that the most salient of the stimuli used in this study were female nude beautiful bodies. Indeed, dimorphism of the body conveys adaptive information relative to fertility, genes quality, dominancy, reproductive potential, and social attraction (Chatterjee, 2014). Beautiful stimuli, particularly female bodies, seem to have high reward-motivating value (Senior, 2003), which in turn may explain the enhanced P300 amplitude (the positivity offset effect; Ito and Cacioppo, 2005). In this regard, it seems to us that the strong use and presence of images of female bodies in overall mass-media contexts to summon viewers' attention might be doing use of the particular salience that this concrete stimulus seems to convey to the human brain, as our data suggest. The interactions at the P300 component also indicated some degree of salience for ugly female bodies -and to a lesser extent to ugly male faces-, indicating that ugly stimuli can also be very salient in this regard.

The connection between the present P300 results and those in the fMRI study by Martín-Loeches et al. (2014) with the present stimuli seems not as straightforward as it was for the P200. Indeed, the frontal distribution of our P300 could harmonize with strong activations in the anterior cingulate cortex and nucleus accumbens in the fMRI study, where they were strongest for beautiful stimuli. It is well known that likely neural generators of the P300 component are anterior cingulate cortex, nucleus accumbens (together with hippocampus) in tasks requiring encoding relevant stimuli based on information about salience, expectancy, and reward (Sabeti et al., 2011; Axmacher et al., 2010). However, these regions displayed a clearly linear pattern in the ugly–neutral–beautiful dimension which does not fit well with the small P300 to some ugly stimuli found here. It might be that other medial frontal regions, such as the mOFC, which were equally activated by both beautiful and ugly stimuli, are also importantly contributing to the present results. Unfortunately, the size of the present sample and the number of electrodes used here do not advice for the use of algorithms to robustly elucidate the neural origins of the present results (Pascual-Marqui, 1999).

Finally, the LPC may reveal a further step in evaluating and examining in deep the salient features of particularly relevant stimuli, i.e., those categorized as very beautiful and very ugly, seemingly. As already mentioned, the LPC seems to index high-level allocation of attention resources, semantic categorization, and the representation of the stimuli in working memory (Cuthbert et al., 2000; Codispoti et al., 2007; Azizian and Polich, 2007). This would be in consonance with the present results, where both beautiful and ugly stimuli appeared highly relevant for the task to be performed by the participants, and may reveal therefore general motivational and attentional processes related with task demands. In the Martín-Loeches et al. (2014) study, both ugly and beautiful stimuli elicited high activations of the medial parietal parts (precuneus, posterior cingulate) as well as lateral inferior parietal areas, which might be in consonance with these areas as contributing to our LPC results. It is a matter of debate which neural sources are generating this component. Assuming that LPC is indexing attention in the visual representation, meaning, and categorization, some studies (Rugg and Curran, 2007; Schendan and Ganis, 2012) propose lateral parietal cortices as likely LPC generators. More recently, in a EEG-fMRI study manipulating working memory load, Luu et al. (2014) suggested that LPC may be reflecting a late neural response in visual association cortices and in memory-related limbic structures (particularly, posterior cingulate and precuneus), as well as an active attentional control in inferior parietal cortices (temporoparietal junction). Importantly, Costanzo et al. (2013) observed other contributing generators of LPC in heteromodal areas of the parietal and temporal cortices, including angular gyrus, in tasks that require assigning stimuli to superordinate semantic categories (esthetic judgment). At this respect, our study and the one by Martín-Loeches have used an esthetic judgment task, what have sense to relate angular gyrus as a likely generator of the LPC. Particularly, in Martín-Loeches et al. (2014), they interpret the activation of a network incorporating the precuneus, middle and posterior cingulate, and the angular gyrus involved in task-relevant and decision-making judgments. Noteworthy, esthetic judgment entails evaluation of internally generated information (internal thoughts, feelings), which requires self-reference (Vogeley and Fink, 2003; Gusnard et al., 2001). In this sense, the default-mode network has been related to the representation of the self-consciousness, and it is likely involved in evaluation of beauty and ugly stimuli in relation to oneself (Vessel et al., 2012). Posterior brain areas underpinning the default-mode network have been located in precuneus, posterior cingulate cortices and angular gyrus, what correspond with neural generators of the LPC (Luu et al., 2014).

3.3. *Possible limitations of the present study*

In the present study, white people evaluated esthetically mostly white people (95.1% of the stimuli). Although the original pool of stimuli included a slightly larger proportion of people from other racial groups, the final preferences of our subjects turned proportions to a mainly within-racial group evaluation. Accordingly, our study cannot be conclusive relative to between-racial esthetic judgments while its findings are limited to people esthetic evaluation by western (European) persons. Possible effects of culture bias on the dynamics of this type of judgments would therefore warrant further explorations. On the other hand, our study is not adding to the literature on sexual attractiveness. Indeed, the task demanded the esthetic evaluation of both male and female stimuli simultaneously. Rather, it is our opinion that the esthetic judgments explored here mainly relate to social relationships. In this regard, our results would primarily be informative on approaching vs. avoiding attitudes relative to a person in sight. In this same line were interpreted a number of main results in Martín-Loeches et al. (2014) study, in which a remarkable de-activation of supplementary motor areas by ugly stimuli was found.

3.4. *Conclusions*

In sum, the present study provides new insights on cognitive and affective processing underlying the esthetic experience of natural objects with deep biological meaning. The visual processing of esthetic images of faces and bodies entails different perceptual, evaluative, and decision-making (esthetic judgment) processes, where attention resources are differently engaged at different processing stages. We suggest that esthetic evaluation of persons seems to largely depend on separable but inherent motivational and affective factors (Cacioppo and Berntson, 1994), which in turn are deeply rooted in evolutionary processes (Grammer and Thornhill, 1994; Rhodes, 2006). This leads to propose that, under evaluative conditions, ugliness and beauty of bodies and faces prompt the activation of both separable and common spread hard-wired networks in the observer's brain. This seems particularly the case when evaluating stimuli with profound biological value, presumably in the frame of social interactions.

4. Experimental procedures

4.1. *Subjects*

Twenty healthy, right-handed participants (equally divided between males and females) in the 18–25 year age range (mean 21.7±2.1 years) were involved in the study. Average handedness scores (Oldfield, 1971) of +76, ranging from +40 to +100. They were undergraduate and had normal or corrected-to-normal vision. None had a history of neurological or psychiatric disorder. The study was performed in accordance with the Declaration of Helsinki, and approved by the ethic committee of the Center for Human Evolution and Behavior, UCM-ISCIII, Madrid, Spain. Participants gave their written informed consent prior to the study and received reimbursal thereafter.

4.2. *Psychophysical testing and scaling*

A pool of 840 images for each esthetic, body part and gender categories (neutral, beautiful and ugly, faces and bodies, male and female) were obtained from internet web pages. The stimuli 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. 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 a 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 detail of all these stimuli was 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 feature such as earrings, scarves, necklaces, tattoos, etc., was 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.

Psychophysical testing was performed by each participant 4±2 days before the EEG session. This test consisted in visualizing the pool of 840 images for each esthetic, body part and gender categories (neutral, beautiful and ugly, faces and bodies, male and female) on a PC monitor. Each image was scored on a scale from 1 to 10. For each participant, an individual selection of stimuli to be classified during the subsequent EEG session was performed, obtaining a total of 32 stimuli per condition, that is, 384 stimuli per subject. Importantly, stimuli in each condition were selected on the extremes (most beautiful and most ugly) and in the middle (neutral), in a continuous of esthetic ratings, being the mean ratings of 1.5 for ugly stimuli, 5.1 for neutral stimuli, and 8.7 for beautiful stimuli.

4.3. *Experimental procedure*

Participants had two successive experimental sessions. Each session consisted on visualizing 24 consecutive blocks containing 8 stimuli, from which 6 stimuli belonged to one esthetic category (for example, beautiful) and two to the other categories (in this example, ugly and neutral) (Fig. 1).

Stimuli in a block were fully randomized. The blocks were counterbalanced along the subjects. Thus, each subject was presented with a different sequence of blocks. Each image was shown for 1 s with an interstimulus interval of 1 second and a half, plus 500 ms of cross-fixation.

During the experiment, the participant sat in a reclining chair inside in a sound-attenuated, electrically shielded and dimly lit room. At the beginning of the experiment, the participants were asked to press one of three buttons depending on their judgement of the current image as beautiful, ugly or neutral. Right and left hand were alternated along the subjects. Moreover, they were encouraged to avoid any muscular movements, including head movements and blinks. They have to maintain the gaze on the centered cross of the monitor between stimulus presentations.

4.4. *EEG recording and data processing*

Continuous EEG was recorded from 27 scalp electrodes. Scalp locations were: Fp1, Fp2, F7, F3, Fz, F4, F8, FC3, FC4, T7, C3, Cz, C4, T8, TP7, CP3, CP4, TP8, P7, P3, Pz, P4, P8, FT7, FT8, O1, and O2 embedded in an electrode cap (Electro-Cap International), and left mastoid (M1), all referenced against the right mastoid (M2). The labels correspond to the revised 10/20 International System (American Electroencephalographic Society, 1991). The vertical electrooculogram (VEOG) was recorded from below vs. above the left eye, whereas the horizontal electrooculogram (HEOG) was recorded from positions at the outer canthus of each eye. Electrode impedances were kept below 3 kOhms. The signals were recorded continuously with a bandpass from direct current (DC) to 70 Hz and a digitization sampling rate of 250 Hz. The data were filtered off-line using a 0.1–40 Hz bandpass.

For each separate time window (detailed below), we analyzed mean voltages using a mixed ANOVA with participant gender (2 levels—male, female) as the between-subjects factor, and esthetic condition (3 levels—beautiful, ugly, neutral) by body part (2 levels—face, body) by image gender (2 levels—male, female) as within-subjects factors. For repeated measures analyses, multivariate statistics were reported. To compensate for a lack of sphericity data, statistical significances in the within-subject factor were corrected by calculating the Greenhouse-Geisser epsilon and reported in each ANOVA test. In all post hoc contrasts, the level of significance was Bonferroni adjusted ($\alpha=0.05$), and the difference of the mean amplitudes and respective significance were also reported.

ERP recordings were analyzed by averaging segments of 1200 ms, beginning 200 ms before stimulus onset. Segments were visual inspected off-line, such that excessive muscle artifacts were manually rejected. Ocular artifacts were automatically corrected following a regression procedure (Gratton et al., 1983). Each experimental category was separately averaged off-line.

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