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Abstract

Although neutral faces do not initially convey an explicit emotional message, it has been found that individuals tend to assign them an affective content. Moreover, previous research has shown that affective judgments are mediated by the task they have to perform. Using functional Magnetic Resonance Imaging in 21 healthy participants, we focus this study on the cerebral activity patterns triggered by neutral and emotional faces in two different tasks (social or gender judgments). Results obtained, using conjunction analyses, indicated that viewing both emotional and neutral faces evokes activity in several similar brain areas indicating a common neural substrate. Moreover, neutral faces specifically elicit activation of cerebellum, frontal and temporal areas while emotional faces involve the cuneus, anterior cingulated gyrus, medial orbitofrontal cortex, posterior superior temporal gyrus, precentral/postcentral gyrus and insula. The task selected was also found to influence brain activity, in that the social task recruited frontal areas while the gender task involved the posterior cingulated, inferior parietal lobule and middle temporal gyrus to a greater extent. Specifically, in the social task viewing neutral faces was associated with longer reaction times and increased activity of left dorsolateral frontal cortex compared with viewing facial expressions of emotions. In contrast, in the same task emotional expressions distinctively activated the left amygdale. The results are discussed taking into consideration the fact that, like other facial expressions, neutral expressions are usually assigned some emotional significance. However, neutral faces evoke a greater activation of circuits probably involved in more elaborate cognitive processing.

Introduction

The ability to recognize affective messages in the face is considered an essential skill in social interaction, not only to establish effective interpersonal communication but also to understand the emotional states of other individuals and predict their social behavior (Ekman 1982; Blair 2003). Many theoretical studies have suggested that this ability has been favored in evolution to confer adaptive advantages in intra-specific social development and cohesion (Fridlund 1994). Consequently, it has also been suggested that a neurobiological structure would have developed that specializes in accurately recognizing and expressing emotional messages, at least those valuable for an individual’s survival, which correspond to the so-called basic emotions (Damasio 1998; Dalgleish 2004).

Therefore, over the past few years through patient studies with cerebral lesions (see e.g., Carvajal et al. 2009) and, especially, after the development of functional and electrophysiological neuroimaging techniques, evidence has been compiled to support the existence of the neural circuits employed to recognize emotions, specifically, emotional facial expressions. The brain regions involved in these circuits are being revealed in increasing detail, and suggest the implication of an extensive interactive network of cerebral structures (Vuilleumier&Pourtois, 2007). Hence, it has been shown that the perception of facial expressions is associated with the activation of areas of the occipital and superior temporal cortex (Labar et al. 2003; Winston et al. 2004), the prefrontal and somatosensory cortex (Esslen et al. 2004; Ioannides et al. 2004; Ishai et al. 2006; Geday et al. 2007); and limbic structures such as the insular cortex, amygdale or posterior cingulated cortex (Kesler-West et al. 2001; Adolphs et al. 2003; Britton et al. 2006).

In spite of evidence to support them, the relationships among these brain regions in the recognition process is not yet clear (Gobbini and Haxby, 2007; Atkinson and Adolphs, 2011). There are important differences in the procedures and the type of stimuli used and, consequently, interesting debates are still underway as to the specific role played by different brain regions and nuclei in the selective recognition of some emotions these (Fusar-Poli et al. 2009a, b; Dima et al. 2011). Other related controversial issues refer to the specificity of brain activation to emotional faces in comparison to neutral faces. To sum up, this refers to whether a neutral face is, in fact, a stimulus without an affective message, compared to facial expressions of emotions. Possibly, viewing an inexpressive face is not really an affectively neutral stimulus and could, therefore, activate some brain circuits shared with those involved in perceiving the facial expression of an emotion. Likewise, in the so-called overgeneralization hypothesis, Zebrowitz (1997), even proposes the existence of a tendency to perceive some neutral face features as emotional expression traits. For example, Phillips et al. (1997) proposes that 100% neutral (muscles relaxed) faces can appear slightly cold or sad. Similarly, when judges must assign emotional categories to facial expressions and neutral faces, they assign an emotional content to neutral facial muscular configurations (Carrera and Fernández-Dols 1994; Carvajal and Iglesias 2006). Taken together, the results of behavioral studies indicate that evaluation of faces tends to be done in terms of the perception of subtle emotional cues (Said et al. 2011).

In accordance with behavioral studies perception of neutral faces would be expected to share a rather similar cerebral activity to that triggered by emotional facial expressions (Schwartz et al. 2003; Ioannides et al. 2004). However, different meta-analytic reviews of the relevant emotion neuroimaging literature have reached somewhat different conclusions regarding which specific neural networks are associated with each basic emotion (Phan et al., 2002; Murphy et al., 2003; Fusar-Poli et al., 2009a, b; Vytal and Hamann, 2010).

These interconnected brain areas could also be differentially activated depending on the specific demands of the task (Atkinson and Adolphs, 2011). Hence, for example, the medial prefrontal cortex has been shown to be differentially activated in tasks that test social decision-making (approachability of the face) versus a cognitive task (gender decision) (Amodio and Frith 2006). More recently, Bzdok et al. (2011) have also shown that brain functional networks activated by neutral faces are different depending on the nature of judgments that subjects have to make. For example, they found that social judgments (attractiveness and trustworthiness) selectively activate amygdale and inferior and ventromedial prefrontal cortex compared to cognitive judgments (age).

Based upon these previous results, our aim is to contribute to current knowledge of the cerebral basis of the recognition of facial expressions. In particular, we are interested in investigating the specificity of the brain activity triggered by emotional expressions and neutral faces. To control the possible modulatory effect of judgments made by the participants we apply the same stimuli with two different tasks, one involving a social judgment (to decide whether the face presented is pleasant or unpleasant) and, another related to a cognitive control condition (to indicate the gender of the shown facial stimuli). By using functional Magnetic Resonance Imaging (fMRI), we compared brain activity to facial expressions of frequent and basic emotions (happiness, anger and sadness) and neutral faces. Also, we compared behavioral responses (reaction times), as a complementary measure of task difficulty (Habel et al., 2007).

We expected neutral and emotional faces to activate rather similar brain areas, but some specific activity to be found. More specifically, we expected emotional faces to evoke a greater activity in areas related with more automatic aspects of emotional response, such as the amygdale. In contrast, neutral faces would not only activate emotion related brain areas, but also regions probably involved in decision making, such as the prefrontal cortex. Also, taking into account previous studies (Bzdok et al., 2011; Said et al., 2011), we would expect to find differences in brain activation and reaction times as a consequence of the task that individuals perform and, more specifically, increases in prefrontal brain activity for social judgments and not for cognitive judgments.

Method

Participants

Nine male and 13 females participated in the study (mean age = 26.68; SD = 4.83; range: 21-38). One subject was subsequently excluded from the analysis due to technical problems. All participants were right-handed, with normal or corrected to normal vision, did not have a current or prior history of neurological or psychiatric illness, and were not taking any medication or illicit substances. Written informed consent was obtained from each participant. They were not paid for their participation. The university research ethics committee granted ethical approval.

Materials and experimental paradigm

Visual stimuli were presented as black and white displays on a uniform white background. Face photographs of eighteen individuals, each displaying a happy, angry, sad or neutral expression, were selected from two standardized set of stimuli (Ekman and Friesen 1975; Bowers et al. 1991); in both cases stimuli were defined by muscular prototypical configurations (in the case of emotional expressions) or by the absence of muscular activity (neutral faces).During fMRI acquisition the stimuli were presented through MRI compatible goggles (VisuaStimDigital, Resonance Technology Inc, Northridge, CA) and optic-fibre button boxes were used to record participant responses. Experiments were performed using SuperLab software (Version 4.5, Cedrus Corp.CA).

Stimuli were presented in a block design, blocked by condition (happy, angry, sad or neutral) to maximize the statistical power (Hall et al. 2010; Jehna et al. 2011). Within each epoch, the valence of the facial expression remained fixed. Each block consisted of 6 stimuli that were presented for 2500 ms with a 500 ms interval.

Subjects were instructed to indicate by pressing one key with each hand whether the image presented was a *man* or a *woman* (gender task), or how *pleasant* or *unpleasant* they thought each image was (social task). A visual instruction text alerted the subject at the beginning of each block which of the two tasks they had to respond. To avoid motor preparation effects, assignment of buttons to response categories was counterbalanced across subjects.

Each run started by viewing a blank screen for 15 s. Then, twenty-four 18 s task epochs (six blocks for each category; three for the gender task, and three for social task) were presented in a fixed pseudorandomized order. The tasks performed were fully counterbalanced across participants to control for any order effects. Twelve rest epochs (15 s cross-hair fixations plus a 3 s instruction text) were presented within each run, counterbalanced to ensure equal presentation before and after each experimental epoch. Previous training with the tasks and the response schedule was performed outside the scanner with a different set of images.

Image Acquisition

The fMRI data were acquired on a 3.0T SignaHDx MR scanner (GE Healthcare, Waukesha, WI) using an eight-channel head coil (GE Coils, Cleveland, OH). Functional images were obtained with a gradient echoplanar sequence using blood oxygenation level-dependent (BOLD) contrast, each comprising a full volume of 40 contiguous axial slices (3mm thickness, 0mm spacing). Volumes were acquired continuously with a repetition time (TR) of 3 s [TE = 31 ms, flip angle = 90, field of view (FOV) = 21.7

cm]. A total of 240 scans were acquired for each participant in a single session (12 min run), with the first five volumes subsequently discarded to allow for T1 equilibration effects. High-resolution T1-weighted spoiled gradient recall (SPGR) anatomical images were also obtained for each subject (184 1.8mm-thick axial images, TR=5.5, TE=2.3, FOV = 24 cm, 256 x 256 matrix).

Data Analysis

Behavioral Data

A repeated-measures analysis of variance (ANOVA) with the four facial expressions (happy, anger, sad and neutral) and the two tasks (social task and gender task) as the within-effect factors was used to compare reaction times.

fMRI Data

The data were analyzed using a general linear model in SPM8 (Welcome Department of Imaging Neuroscience, London, UK, www.fil.ion.ucl.ac.uk/spm/) implemented in MATLAB 7.10 (Mathworks, Inc., Sherborn, MA). Individual scans were realigned, slice time corrected, normalized, and spatially smoothed by a 6 mm FWHM Gaussian kernel using standard SPM methods. The voxel dimensions of each reconstructed scan were 2 x 2 x 2 mm. Population inference was made through a two-stage procedure. At the first level we specified in a subject-specific analysis where the BOLD response was modeled by a boxcar waveform of 18 s representing a single block, convolved with a canonical hemodynamic response function plus temporal and dispersion derivatives. Rest condition served as baseline. Statistical parametric maps of the t statistic were generated for each subject and condition, and the contrast images were stored. For each individual, we determined the effect of the following contrasts of interest: happy-angry; happy-sad; angry-sad. These analyses revealed no statistically significant differences ($p < 0.05$ FWE) in any case. Then we focused on voxels that showed differences between “emotion” and “neutral” conditions and between these and rest epoch. We defined the “emotion” effect as the brain activation evoked by stimuli showing happy, angry and sad faces collapsed together. On the other hand, the neutral condition comprised only neutral faces.

In a second level random effects analysis, a 2x2 (task by emotion) ANOVA model was used. We constructed an F contrast to test for the main effects of task and emotion and a task by emotion interaction, which indicates the extent to which the difference between activities when seeing both emotional conditions (emotion vs. neutral) may vary while performing each task. In order to correct for multiple comparisons in interpreting these results, two strategies were used. First, we used a threshold of p<0.05 Familywise Error Rate (FER) corrected for multiple comparisons for the entire brain volume to assess the main effects of task and emotion. Then, to assess the interaction effect (task x emotion), specifically for amygdale, a small volume correction (SVC) with a sphere of 10 mm radius was used. In addition, we tested the similarities in brain activations between two contrasts performed: neutral faces>rest, and emotional faces>rest. In order to test this possibility a conjunction analysis was performed.

The surviving activated voxels were superimposed on high-resolution structural magnetic resonance (MR) scans of a standard brain (Montreal Neurological Institute, MNI). Anatomical identification was performed with reference to the Talairach Daemon Software (http://www.talairach.org/), and AAL from MRIcro software (http: //www.sph.sc.edu/comd/rorden/mricro.html).

Results

Behavioral Data

Means and standard deviations of reaction times to different faces in both tasks are recorded in Table 1. In addition to the main effect of the task ($F(1,20)=16.89$, $p<.001$), the 2 (task) x 4 (emotion) ANOVA revealed a significant interaction between task and emotion ($F(1,20)=5.35$, $p<.05$); subsequent Bonferroni-test analyses only showed a significant effect of the emotion in the social task, where neutral faces displayed a longer average reaction time than happy, anger and sad faces ($ps< .05$).

Insert Table 1 around here

fMRI Data

Functional images were analyzed by SPM8 using a general linear model applied at each voxel across the whole brain.

First, brain activity associated with rest epoch was subtracted from that evoked by neutral and emotional faces. The random effects model revealed significant activations ($p<0.05$ FWE corrected) in a wide number of brain areas. Thus, neutral faces compared to rest epochs activated middle and inferior frontal cortex, primary motor cortex (precentral gyrus), parietal inferior and occipital cortex, fusiform gyrus, amygdale, putamen and cerebellum. On the other hand, emotional faces compared to resting condition were associated with increased activity in a rather similar network, and adding insula and hippocampus. In order to test the similarities in brain activations between these two contrasts (neutral faces-rest, and emotional faces-rest) a conjunction analysis was performed. This analysis revealed a wide pattern of activation with a predominance of the right hemisphere ($p<0.05$ FWE corrected; see table 2).

Insert Table 2 around here

Then, when the brain activity associated with viewing neutral faces was compared with that associated with viewing emotional stimuli, the random-effects model revealed significant activation clusters surviving a threshold of $p<0.05$ FWE corrected, described in Table 3.

Insert Table 3 around here

The results showed more pronounced activation of facial expressions of emotion than neutral faces in the left cuneus, right superior temporal gyrus, right cingulate gyrus, bilateral medial frontal gyrus, left middle frontal gyrus, bilateral precentral gyrus, right postcentral gyrus and right insula; and more pronounced activation of neutral expression than emotional faces in prefrontal regions (bilateral superior frontal gyrus, right inferior and middle frontal gyrus), cerebellum, left superior temporal gyrus, bilateral parahipocampal gyrus, left lobule occipital, right inferior parietal lobule and left mammillary body (Figure 1).

Insert Figure 1 around here

Then, we compared the activation associated with each of the two tasks used (Figure 2).

Insert Figure 2 around here

The social task compared with the gender task was associated with increased activation in a several prefrontal areas (bilateral superior and inferior frontal gyrus and right middle frontal gyrus); the gender task compared with the social task showed an increased pattern of activity in the right cingulate gyrus and right semantic representation areas (middle temporal gyrus and inferior parietal lobule). In table 4 we list clusters where SPM{F} for the main effects of task reached $p<0.05$ (FWE corrected).

Insert Table 4 around here

An interaction between task and facial expression was identified in the left orbitofrontal cortex. Specific contrasts indicated that the effect of the interaction was due to a differential response during the social task; in particular, in comparison with emotional faces, there was greater left middle frontal gyrus activity (BA=46; Talairach, X=-54, Y=18, Z=6; F= 24.26; z-score= 4.60) while participants processed neutral faces. A $p<0.05$ (FDR corrected) was applied for the interaction analyses. Interaction effects were also found (SVC using a 10 mm sphere). A cluster comprising 37 voxels, within the search area survived the correction located in the left amygdale (Talairach, X=-18, Y=-2, Z=-24; F=17.41; z-score=3.89). The interaction effect was due to a differential response during the social task; in particular, emotional faces showed greater activity than neutral faces.

Discussion

The present study used functional magnetic resonance imaging to examine the neural substrate associated with the perception of facial expressions of basic emotions. We focused our attention on the evaluation of faces with neutral expressions compared to emotional expressions. Neuroimaging data obtained suggest that the perception of neutral faces is related to the recognition of emotional facial expressions. Both rely on a rather similar face-responsive network, which includes areas that seem to be relevant in processing identity, and others involved in detecting emotion. In general, we observed a wide and common right lateralized activation pattern in response to emotional expressions and neutral faces, which included frontal, parietal, occipital and temporal regions. Nonetheless, our findings also revealed divergence in the specific pattern of activation during the processing of each type of facial stimuli, as well as a marked variability in the regional activation between the tasks we employed.

First, we identified by conjunction analysis the set of areas of face-responsive, independently of the emotional content and task. The results revealed a widespread network distributed across the right hemisphere, which included the occipital face area (OFA), frontal gyrus (middle and inferior), inferior parietal lobule, middle temporal gyrus, precentral gyrus and uncus. In addition, the cerebellum and the insula were also active in both hemispheres during facial processing; while, in the left hemisphere, the only region activated was the medial frontal gyrus. These areas are included in the core and extended face processing brain system, according to the Haxby et al. model (Haxby et al. 2000; Gobbini and Haxby 2007). Furthermore, these data support the proposed right hemispheric dominance in face perception (Murphy et al. 2003).

Some of the regions identified by the conjunction contrast have been associated either with identity or emotional face processing in a wide range of studies (LaBar et al. 2003; Calder and Young 2005; Ishai et al. 2005; Atkinson and Adolphs 2011; Said et al. 2011). Hence, OFA is the first stage in a hierarchical faces perception network and represents facial components, so is essential for facial identity (Li et al. 2010; Pitcher et al. 2011). Complementarily, the posterior portion of the middle temporal gyrus has been associated with the perception of facial expressions (Hein and Knight 2008; Said et al. 2010). These data show that when individuals are confronted with a face, including a neutral face, areas related to facial expression are also activated, together with those involved in identity perception. We could, therefore, deduce that when we perceive a neutral face, as well as processing its identity, we can also try to assign it an emotional value, which is logical given the importance of this information in human social interaction (Zebrowitz 1997).

Neutral and emotional activation

However, our aim was mainly to identify brain differences as a function of the neutral and emotional facial perception. In this line, we observed that viewing neutral faces evokes coactivations between a network of frontal cortex and several other areas, including superior temporal gyrus (STS), cerebellum, parahippocampal gyrus and mammillary body compared to facial expressions. Most of these areas have recently been referred to as integrated in an extended system for both, face and voice perception (Ethofer et al., 2013). So, according to this wide network processing neutral faces seems to evoke a complex representation.

Regarding the prefrontal cortex, we particularly found dorsolateral, ventrolateral and orbitofrontal activity. All together, the lateral/orbitofrontal cortex, has been implicated in several psychological functions, such as encoding novel information, evaluative processing, decision-making and face processing (Rolls, 2004; Ishai 2007). Additionally, each specific frontal region reveals dissociable roles: motor functions of the supplementary motor area are well documented, and activity in this area may reflect motor imagery and inhibited motor output during internal simulation (Nachevet al. 2008). Although this area has been found to be commonly activated across different emotional faces, a greater response to neutral faces has also been reported *(*Fusar-Poli et al., 2009a, b). Regarding the orbitofrontal cortex (OFC) activity, it has been suggested to constitute a neural interface linking sensory areas with brain regions implicated in the generation of behavioral responses, such as the above mentioned supplementary motor area. The OFC has been implicated in a broad range of functions including a key role for the active judgment of social signals (Zald et al., 2012). THE OFC has also been attributed a crucial role in the top-down processing of faces regulating the activities of the OFA and the fusiform face area (FFA). This top-down face processing is required to interpret ambiguous faces stimuli, imagined face or to detect impoverished face stimuli (Li et al., 2010).

In addition, in our study, the temporal pole (anterior portion of superior temporal gyrus and parahippocampal cortex) responded more actively to neutral faces. The parahippocampal gyrus, has been consistently associated with the perception of human faces and the superior temporal gyrus (STG) integrates into the superior temporal sulcus (STS), a cortical region especially involved in the interpretation of faces (Haxby et al., 2000). In the same line, it has recently been proposed that the role of the STS in human cognition and emotion is to process "social attention" which is a crucial human skill for making inferences with respect to others' goals, intentions and actions (Hein and Knight 2008; Iidaka 2012). It seems, therefore, that the perception and judgment of neutral faces is a complex social task that involves greater cognitive effort than emotional faces regardless of the type of task performed.

Interestingly, we also found an increased brain activity in mammillary bodies and cerebellum to neutral faces in comparison to emotional expressions. Both areas have been consistently related with emotional and memory processing in different studies, but interpretation of their role in facial recognition remains unclear (Fusar-Poli et al. 2009a, b). Regarding mammillary bodies, clinical studies repeatedly show that lesions in this diencephalic region can impair recognition memory (Aggleton et al. 2011), but their role in emotional recognition has not been determined. A recent meta-analysis of neuroimaging studies, examining sex differences as a function of positive vs. negative emotional valence, showed men´s and women's responses to all emotional stimuli in an extended cluster of regions including the mammillary body (Stevens and Hamman, 2012).It has also been described that stroke seemingly confined to mamillothalamic tract and anterior parts of lateral thalamus produced visuospatial memory deficits, including poor face recognition (Daum and Ackermann 1994). Also, Beglinger et al. (2006) observed severe and persistent recall deficits in the Warrington Recognition Memory Test for faces and words in a patient with bilateral loss of the mammillary bodies. Although these data suggest a role for mammillary bodies in emotional processing and face recognition, to our knowledge, this is the first neuroimaging study that shows its implication in face processing.

Otherwise, our results further support the involvement of the cerebellum in facial processing. We found a neural response in the cerebellum in conjunction analysis, but also, the right cerebellum was activated significantly more in response to neutral faces than to emotional faces. The unspecific activation to different faces and facial expressions points to a general role of the cerebellum in cognitive and emotional processing (Turner et al. 2007). However, recent clinical and neuroimaging research has tried to establish its precise contribution to each of the non motor functions. On the one hand, several studies indicate that the cerebellum might play a role in experiencing and controlling emphatic emotions. Cerebellar regions are required during subliminal and task-irrelevant emotional face processing, which could explain cerebellar activation found in conjunction analysis (Pantazatos et al., 2012). On the other hand, Schraa-Tam et al. (2012) suggest the potential role of the cerebellum in cognitive control for goal-directed behavior as required, for example, in observing and reacting to another person's expressions. Additionally, reciprocal connections between the cerebellum, the dorsolateral prefrontal cortex and anterior temporal lobe have been described (D'Angelo and Casali, 2012), Precisely, these circuits coincide with activations we have found to neutral faces and, as discussed before, may contribute to cognitive control and decision-making to complex stimuli.

By contrasting to the processing of neutral faces, emotional faces seem to require the integrated activity of frontooccipital regions and limbic regions. During the neural coding of facial affect, five specific areas are concomitantly activated, the cuneus, the anterior cingulate gyrus, pre/postcentral gyrus, insula and medial OFC, to a greater extent than neutral faces. The cortical network identified as contributing to the processing of emotional faces is highly consistent with a number of previous studies (Fusar-Poli, 2009a, b).

With respect to the insular cortex and anterior cingulated gyrus, both limbic regions have been implicated in the rapid processing of salient facial emotional information (Fan et al., 2011). For the insular activity, this has been reported during the processing of negative facial expression, like disgust and angry faces (Fusar-Poli et al., 2009b) and has, recently, been implicated in the processing of unattractiveness and negative personality faces (Tsukura et al., 2012). Regarding the cingulated cortex, anterior regions are considered as “transition regions” wherein cognitive and affective processes are integrated (Torta and Cauda 2011), and are also involved in rapid processing of facial emotional information (Fan et al. 2011). The cingulated cortex is a richly interconnected heterogeneous region and Vogt et al. (2005) suggest that different parts of the cingulate cortex could be related in activities that are shared by several tasks rather than by specific ones. To support this idea it has been suggested that the anterior cingulated cortex works together with limbic sensory and motor regions and plays a complementary role in the production of interoceptive and subjective feelings (Torta and Cauda 2011),

Also, we observe that the cuneus, motor, pre-motor and nearby somatosensory cortex show functional coactivation during the perception of facial expressions. These regions may have a role in emotion recognition through the mirror neuron system. In particular, cuneus activation has been related to the theory of mind during imitation (Vrticka, et al., 2013). When simply looking at expressive faces images, people mimic the facial expression, by producing microexpressions (Dimberg et al. 2000). It could, therefore, be suggested that recognition of the expression and its subsequent imitation would occur more automatically in response to facial expressions with a clear emotional content than to neutral faces. In fact, we found motor cortex activity only to emotional faces, supporting this possible active simulation processes. In the same line, a greater response has been described in the left motor cortex to fearful than to neutral faces in a priming task (Fan et al. 2011).

It is also worth noting STS and OFC activity in emotional as well as in neutral face processing, although different subregions are implicated in one or another. Consistent with previous research, while neutral faces recruit anterior temporal areas, posterior STS is involved in a response to emotional faces. The latter has been related to the processing of changeable features of faces, such as the expression (Hein and Knight, 2008). Regarding the prefrontal cortex, in contrast to the right lateralized pattern to neutral faces, to facial expressions we located the involvement of medial regions that have a well-established role in emotional processing (Phan et al., 2002; Phillips et al., 2003; Dima et al., 2011). Recently, by means of meta-analytic connectivity modeling, a differentiation has been established between the pattern of functional connectivity for the medial and for the lateral OFC (Zald et al., 2012). Lateral OFC showed coactivations with a network of prefrontal regions and areas involved in cognitive functions we found to be involved in processing neutral faces in this work. In contrast, medial OFC showed connectivity with autonomic and limbic regions. Taken together, these results indicate a relevant role for the prefrontal cortex in the perception of emotional and non-emotional faces, and support the existence of different functional circuits in this intricate orbitofrontal region.

Task effects

In this work we have also observed a clear modulation of the activity in different brain regions, according to the type of perceptual decision-making tasks we employ. On comparing the tasks, we observe that the social task evokes greater activity in the superior, middle and inferior frontal gyrus while the gender task differentially requires the posterior cingulate, inferior parietal lobule and middle temporal gyrus.

The group of areas recruited by the social task (all located in the prefrontal cortex) could be linked to the perceptual representation of faces for the generation of knowledge in relation to its social significance. Supporting this, it is well known that the prefrontal cortex has been implicated in many cognitive functions, including holding spatial information, working memory, response selection, and the verification of representations that have been retrieved from long-term memory (Ramnani and Owen, 2004). Furthermore, our finding concurs with the results of a recent meta-analysis highlighting the bilateral activation pattern at the level of the frontal cortex, during comprehension of social signals in facial expressions (Sabatinelli et al., 2011). Thus, in our work we locate several dorsolateral prefrontal cortex areas, which have been related to featural aspects (e.g., shape of the mouth) and the configural processing of faces (spatial interrelationships between features) (Renzi et al., 2013). Another of the most active cortical areas in social task was the middle prefrontal cortex, which has also been implicated in emotional processing (Fan et al., 2011). In addition, the inferior frontal gyrus handles semantic information and several studies have shown that it can be activated by expressive face processing (Ishai et al., 2002; Fusar-Poli et al., 2009b). This set of data support the observations made by Dima et al. (2011) highlighting the role of the prefrontal cortex during affective processing, and questioning the prevailing amygdalocentric model of affective processing. Based on the important role of the frontal region in social tasks and its complex functions, it may be assumed that the attribution of a pleasant or unpleasant character to a face conveys it a higher-level representation than a more automatic and effortless gender decision.

Support for the idea that this frontal activation may be related to cognitive load may also come from the behavioral data, specifically when neutral faces are presented. The participants showed greater reaction times to neutral versus emotional faces in social task. We also found that neutral faces activate dorsolateral frontal regions particularly engaged in the assessment of ambiguously expressed emotion (Nomura et al., 2003). On the basis of this evidence, we can argue that processing neutral faces in the social task may involve more executive control than the gender task.

Regarding the gender task, Kaul et al. (2011) suggest that information about facial gender is represented in almost all regions of the face network. Nonetheless, our data show that some regions, such as the posterior cingulated and the temporal parietal junction, with well known strong functional connections between them, may play a more important role in the gender decision task. Activation of these areas may reflect visuospatial processing and episodic memory involvement during evaluation of the traits of each gender. Supporting this idea, the activated posterior parts of the cingulated have been associated with saliency detection, visuospatial and episodic memory functions and face discrimination (Torta and Cauda 2011). Previously we have mentioned a preferential participation of the anterior region characterized by its involvement in attention and rapid processing of salient facial emotional information (Fan et al. 2011). Then, the cingulated cortex would be considered as a higher order associative area which would explain its great significance in the gender task and also in the analysis of emotional faces.

In any case, this finding, together with that previously mentioned, suggests that the processing of facial expressions depends on broad neural circuits and areas with interactive and complementary functions which may vary according to task or context (Vuilleumier and Purtois 2007; Atkinson and Adolphs 2011). To conclude, the results of this work suggest that emotionally inexpressive faces are not perceived very differently from emotional facial expressions and their recognition requires at least a partially shared neural network. However, neutral faces activate other frontal and temporal brain regions that could reflect a more elaborate cognitive processing not required for facial expressions of basic emotions, and emotional faces have been found to activate some specific limbic brain areas. We have observed these differences independently of the task performed, although to a greater extent when the participants are required to make an explicit social judgment. We, therefore, consider that further studies are needed to ascertain the coordinated role of the broad cluster of different areas and neural networks implicated in facial and emotional recognition.

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Table 1. Mean and Standard Deviation of Reaction Times (milliseconds) to emotions and neutral faces in the social and gender tasks.

	Faces			
Task	Neutral	Happiness	Anger	Sadness
Social	1139.2 (304.5)	890.9 (199.5)	966.5 (214.3)	998.9 (223.7)
Gender	877.6 (195.5)	861.4 (201.2)	835.9 (197.3)	883.4 (234.4)

Table 2. Results of the fMRI conjunction analysis (neutral faces-rest and emotional faces-rest). L: left, R: right, Mid: Middle

Brain Regions activated	Hemisphere	BA	Nº Voxels	Talairach			T	z-score
				x	y	z		
Occipital lobe	R	18	6160	14	-102	6	12.62	>8
Occipital lobe	L	18		-16	-102	4	12.16	>8
Lingual Gyrus	R	17		12	-98	-12	11.55	>8
Middle Frontal Gyrus	R	46	65	46	26	24	5.58	5.32
Middle Frontal Gyrus	R	9		48	30	32	5.15	4.94
Middle Frontal Gyrus	R	9	27	56	14	34	5.39	5.15
Medial Frontal Gyrus	L	6	683	-8	2	56	8.17	7.43
Medial Frontal Gyrus	R	6		6	0	60	7.78	7.13
Superior Frontal Gyrus	R	6		10	8	56	7.06	6.55
Inferior Frontal Gyrus	R	9	134	44	4	28	5.91	5.60
Precentral Gyrus	R	6	173	44	-8	60	6.04	5.71
Precentral Gyrus	R	6		52	0	46	5.96	5.64
Precentral Gyrus	R	6		48	0	56	5.47	5.22
Precentral Gyrus	L	6	2	-48	-8	54	4.93	4.74
Precentral Gyrus	L	6	5	-42	-10	60	5.27	5.04
Inferior Parietal Lobule	R	40	26	48	-46	46	5.36	5.12
Inferior Parietal Lobule	R	40	192	34	-54	42	5.94	5.63
Superior Parietal Lobule	R	7		34	-64	50	5.34	5.10
Superior Temporal Sulcus	R	21	83	48	-46	2	5.87	5.56
Uncus	R	28	30	18	-6	-24	6.07	5.74
Insula	L	13	32	-34	14	12	5.60	5.33
Insula	L	13	4	-44	-6	10	5.13	4.92
Insula	R	13	8	34	20	4	5.13	4.92
Cerebellum	L		88	-10	-78	-36	5.77	5.48
Cerebellum	L			-10	-86	-28	5.55	5.29
Cerebellum	L			-6	-84	-18	5.18	4.96
Cerebellum	R		10	8	-32	-8	5.20	4.98

Table 3. Clusters showing main effects of emotion.. R: rightL: left, R: right.

Greater activity in response to facial expressions of emotions than neutral faces

Brain Regions activated	H	BA	Nº Voxels	Talairach			T	z-score
				X	Y	Z		
Precentral Gyrus	R	4	25	42	-18	42	5.35	5.12
Precentral Gyrus	L	4	42	-40	-18	36	6.03	5.71
Postcentral Gyrus	R	5	84	22	-44	66	6.03	5.71
Anterior cingulate	R	32	149	8	40	4	6.57	6.16
Cuneus / lob occipital	L	18	7038	-12	-74	24	9.09	>8
Superior Temporal Gyrus	R	22	224	58	-2	2	6.47	6.08
Medial Frontal Gyrus	L	10	39	-10	54	-4	5.59	5.32
Medial Frontal Gyrus	R	10	79	6	56	- 6	6.0	5.68
Middle Frontal Gyrus	L	6	90	-24	14	52	6.41	6.03
Insula	R	*	69	36	-14	2	6.08	5.75

Greater activity in response to neutral faces than facial expressions of emotions

Brain Regions activated	H	BA	Nº Voxels	Talairach			T	z-score
				X	Y	Z		
Superior Temporal Gyrus	L	38	1157	-50	16	-8	8.20	7.46
Inferior Frontal Gyrus	R	47	3699	38	22	-4	9.75	>8
Superior Frontal Gyrus	L	6	1290	-42	-12	62	7.89	7.23
Superior Frontal Gyrus	R	6	1610	4	6	60	9.67	>8
Superior Frontal Gyrus	R	10	70	34	56	26	6.28	5.92
Inferior Frontal Gyrus	L	10	58	-48	46	-2	6.40	6.02
Middle Frontal Gyrus	R	11	43	46	46	-10	5.79	5.50
Cerebellum	R	*	8214	36	-52	-34	11.31	>8
Mammillary Body	L	*	7	-8	-6	-10	5.07	4.87
Parahipocampal Gyrus	L	34	205	-16	-6	-22	7.53	6.94
Parahipocampal Gyrus	R	28	88	16	- 6	-24	7.13	6.62
Lob occipital	L	18	94	-16	-102	4	8.19	7.45
Lingual Gyrus	L	18	38	-8	-100	-10	7.08	6.59
Inferior Parietal Lobule	R	7	68	34	-56	44	5.96	5.65

Table 4. Clusters showing main effects of task. L: left, R: right

Greater activity in response to social task than gender task

Brain Regions activated	He	BA	Nº Voxels	Talairach	T	z-score
				X Y Z		
Superior Frontal Gyrus	R	8	39	6 46 46	6.48	6.09
Superior Frontal Gyrus	L	8	360	-2 24 50	7.25	6.72
Superior Frontal Gyrus	L	6	25	-10 12 64	6.07	5.74
Superior Frontal Gyrus	R	6	40	12 22 62	6.06	5.73
Middle Frontal Gyrus	R	9	380	54 14 32	6.94	6.47
Superior Frontal Gyrus	R	10	15	20 58 22	5.19	4.98
Superior Frontal Gyrus	L	45	415	-54 18 6	7.06	6.57
Inferior Frontal Gyrus	R	45	154	54 28 2	6.80	6.35

Greater activity in response to gender task than social task

Brain Regions activated	H	BA	Nº Voxels	Talairach	T	z-score
				X Y Z		
Posterior Cingulate	R	31	78	8 -30 46	6.03	5.71
Superior Temporal Gyrus	L	22	14	-66 -34 12	5.05	4.85
Inferior Parietal Lobule	R	40	21	66 -26 24	5.59	5.33
Middle Temporal Gyrus	R	21	20	68 -28 2	5.76	5.47
Caudate	R	*	4	20 -40 12	5.16	4.95

Figure 1: Group activation map showing activated brain regions in emotion. Neutral>Emotion is shown in red. Emotion>Neutral is shown in blue. Images thresholded at FWE p<0.05. Neurological convention is followed (left side of the brain is shown on the left side of the figure). Results are visualized using xjView toolbox (http://www.alivelearn.net/xjview).

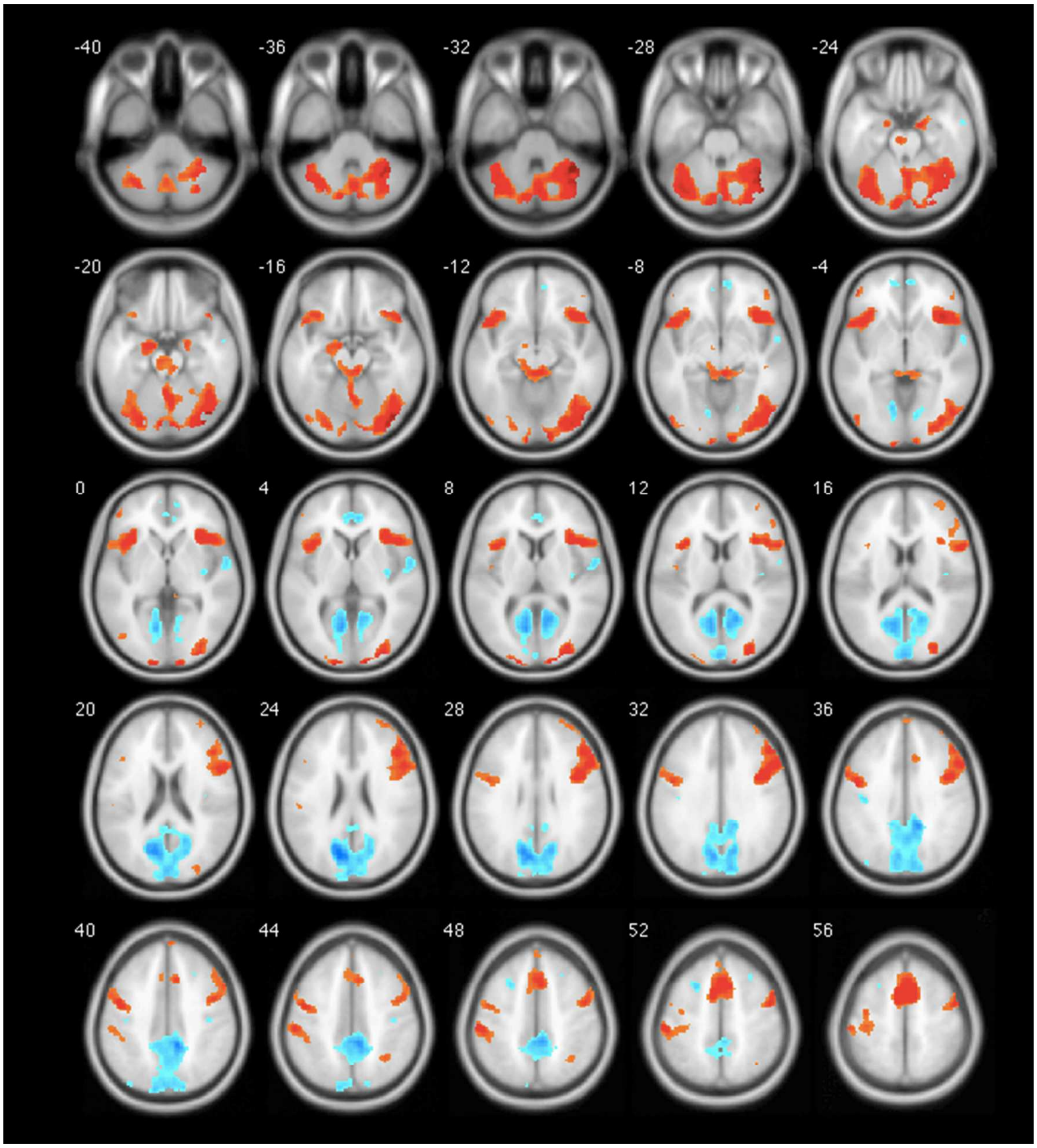

Figure 2: Group activation map showing activated brain regions in tasks. Social>Gender is shown in blue. Gender>Social is shown in red. Images thresholded at FWE p<0.05. Neurological convention is followed (left side of the brain is shown on the left side of the figure). Results are visualized using xjView toolbox (http://www.alivelearn.net/xjview).