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Contributions of stimulus valence and arousal to visual activation during emotional perception

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Abstract

Neuroimaging experiments have revealed that the visual cortex is involved in the processing of affective stimuli: seeing emotional pictures leads to greater activation than seeing neutral ones. It is unclear, however, whether such differential activation is due to stimulus valence or whether the results are confounded by arousal level. In order to investigate the contributions of valence and arousal to visual activation, we created a new category of "interesting" stimuli designed to have high arousal, but neutral valence, and employed standard neutral, unpleasant, and pleasant picture categories. Arousal ratings for pleasant and neutral pictures were equivalent, as were valence ratings for interesting and neutral pictures. Differential activation for conditions matched for arousal (pleasant vs neutral) as well as matched for valence (interesting vs neutral) indicated that *both* stimulus valence and arousal contributed to visual activation.

Introduction

Emotional processing involves a network of brain regions, including the amygdala, the orbital and ventromedial sectors of the prefrontal cortex, the anterior cingulate cortex, as well as the temporal lobe (Davidson and Irwin, 1999; Lane and Nadel, 2000; Phan et al., 2002). Neuroimaging experiments have revealed that the visual cortex is also involved in the processing of affective stimuli. Seeing emotional pictures and words leads to greater activation in visual cortex than seeing neutral ones (Lang et al., 1998; Lane et al., 1997a, 1997b, 1999; Taylor et al., 1998, 2000, Breiter et al., 1996, Moll et al., 2002a, 2002b; Morris et al., 1998; Tabert et al., 2001; Vuilleumier et al., 2001; Rotshtein et al., 2001; Pessoa et al., 2002a). Both posterior occipital visual processing areas, such as V1/V2, and more anterior ventrotemporal regions, such as the fusiform gyrus, exhibit activation when emotional and neutral conditions are contrasted. Enhanced visual processing associated with seeing emotional stimuli may be associated with increased perceptual sensitivity to events of importance to the organism (Anderson and Phelps, 2001; Pessoa et al., 2002b). Thus, it is important to determine the factors underlying visual cortical activation during emotional perception.

Emotional and neutral pictures differ not only in terms of valence, but may also differ in terms of arousal level (Osgood and Tammenbaum, 1957). Thus, it is unclear whether the differential visual activation observed in neuroimaging studies is due to stimulus valence or whether the results are confounded by arousal level. This issue is further compounded by the observation that pictures with strong valence are also rated as highly arousing [Lang et al., 1995; Center for the Study of Emotion and Attention (CSEA NIMH), 1999; Lang et al., 1999]. Thus, it is important to try to unravel the contributions of valence and arousal during emotional picture processing (see also Lane et al., 1999).

In the present study, to investigate the contributions of valence and arousal to visual cortical activation, subjects viewed neutral, pleasant, unpleasant, and well as "interest-

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ing" pictures (with high arousal but neutral valence). If visual activity due to emotional perception were driven by valence, the contrast of conditions matched in arousal level would produce valence-related differential activation. At the same time, if visual activity were driven by arousal, the contrast of conditions matched in valence would produce arousal-related differential activation. It is, of course, possible that both valence and arousal contribute to visual cortical activation during emotional perception, in which case both types of contrast would lead to differential visual activation.

Methods

Subjects

Eight healthy, right-handed volunteers participated in the study (two women; age ranging from 21 to 31). Participants reported no history of neurological or neuropsychiatric disorder and were not under any medication. Data from two participants were discarded because of excessive head motion during scanning. The study was conducted in the Hospital Barra D'Or, Rio de Janeiro, Brazil, and approved by the hospital's Institutional Review Board and Ethics committee.

Data acquisition

The study was performed on a 1.5 MR scanner (Siemens Vision, Erlangen, Germany). Anatomical data consisted of 128 high-resolution gradient-echo T1-weighted volumetric images (slice thickness = 1.25 mm). Functional images covering nearly the whole brain were acquired across 16 slices parallel to the plane of the anterior and posterior commissures with echoplanar BOLD imaging (TR/TE = 4980/66 ms, flip angle = 90°, matrix size = 96 × 128, FOV = 256 mm, thickness/gap = 5/1.25 mm). With these parameters, in all cases our functional scans missed no more than 10 mm of the most superior part of the brain. Head movements were restrained by foam padding. Two hundred eighty-eight functional volumes were acquired for each subject in a single run that lasted approximately 23 min. Stimulus presentation and functional data collection were synchronized.

Experimental design

Subjects viewed static, colored pictures by way of magnetically shielded LCD goggles (Resonance Technologies, Inc, Northridge, CA). Images were delivered by a computer running custom-made visual presentation software. Four sets of 24 pictures were used: unpleasant, pleasant, neutral, and "interesting." Stimuli were presented in a blocked fashion with three pictures per block. Each image, which was presented only once during the experimental session, was displayed for 5 s (i.e., one TR), such that each block lasted 15 s. There were a total of eight blocks for each picture category presented in random order. A white cross-hair fixation on a black background was displayed for 15 s between each block (to allow the hemodynamic response to return to baseline). Participants were told to attend to each image and to apprehend its meaning.

Unpleasant, pleasant, and neutral images were selected from the International Affective Picture System (IAPS), a collection of standardized color photographic material [Center for the Study of Emotion and Attention (CSEA NIMH), 1999; Lang et al., 1999]. To create a new category of highly arousing but neutral-valence pictures ("interesting"), additional images were obtained from sources such as the World Wide Web and photography books. The images included, but were not restricted to, surreal pictures and included scenes (8), objects (4), faces (7), hands (4), human bodies (13, 2 with distinguishable faces), and animals (2); see Fig. 1. In a separate behavioral session, a group of 30 Brazilian subjects rated the pictures in terms of degree of surreal content and degree of clarity. A total of 50 and 82% of the interesting pictures were rated as having moderate or high surreal content and clarity, respectively, whereas 5 and 85% of the other categories were rated in this manner. Finally, it should be mentioned that interesting, pleasant, and unpleasant images contained similar number of faces or bodies: Interesting: 9 faces/11 bodies (or body parts, but no distinct faces); Pleasant: 10/2; Unpleasant: 7/8; values for the neutral category were lower: 2/3.

The IAPS database provides normative ratings in the dimensions of valence (ranging from unpleasant to pleasant) and arousal (ranging from calm to excited). In a separate behavioral session, a group of 25 Brazilian volunteers rated the pictures in terms of valence and arousal, according to the IAPS procedure (Lang et al., 1999). Subjects were seated in rows facing the screen on which the images were projected. Initially, they read instructions and viewed examples of ratings. The experiment began with a preparation slide ("Get ready to rate the next image"), which was presented for 5 s. Then images were presented for 6 s. During the 10-s interval between pictures, participants were asked to rate the picture (in a rating booklet) on the dimensions of valence and arousal using the Self-Assessment Manikin (SAM), an affective rating system devised by Lang (1980). In this system, ratings of valence are indicated by 5 graphical representations of facial expressions ranging from a severe frown (most negative) to a broad smile (most positive). For arousal, the manikin varies from a state of low to high agitation. Participants may select any of the five figures, or boxes in between, on a nine point rating scale for each dimension. In the valence dimension 9 represents the extreme of pleasantness and 1 the extreme of unpleasantness. For the arousal dimension ratings are such that 9 represents a high rating and 1 represents a low rating. The statistical threshold for significance employed for the behavioral data was a P value of 0.05.

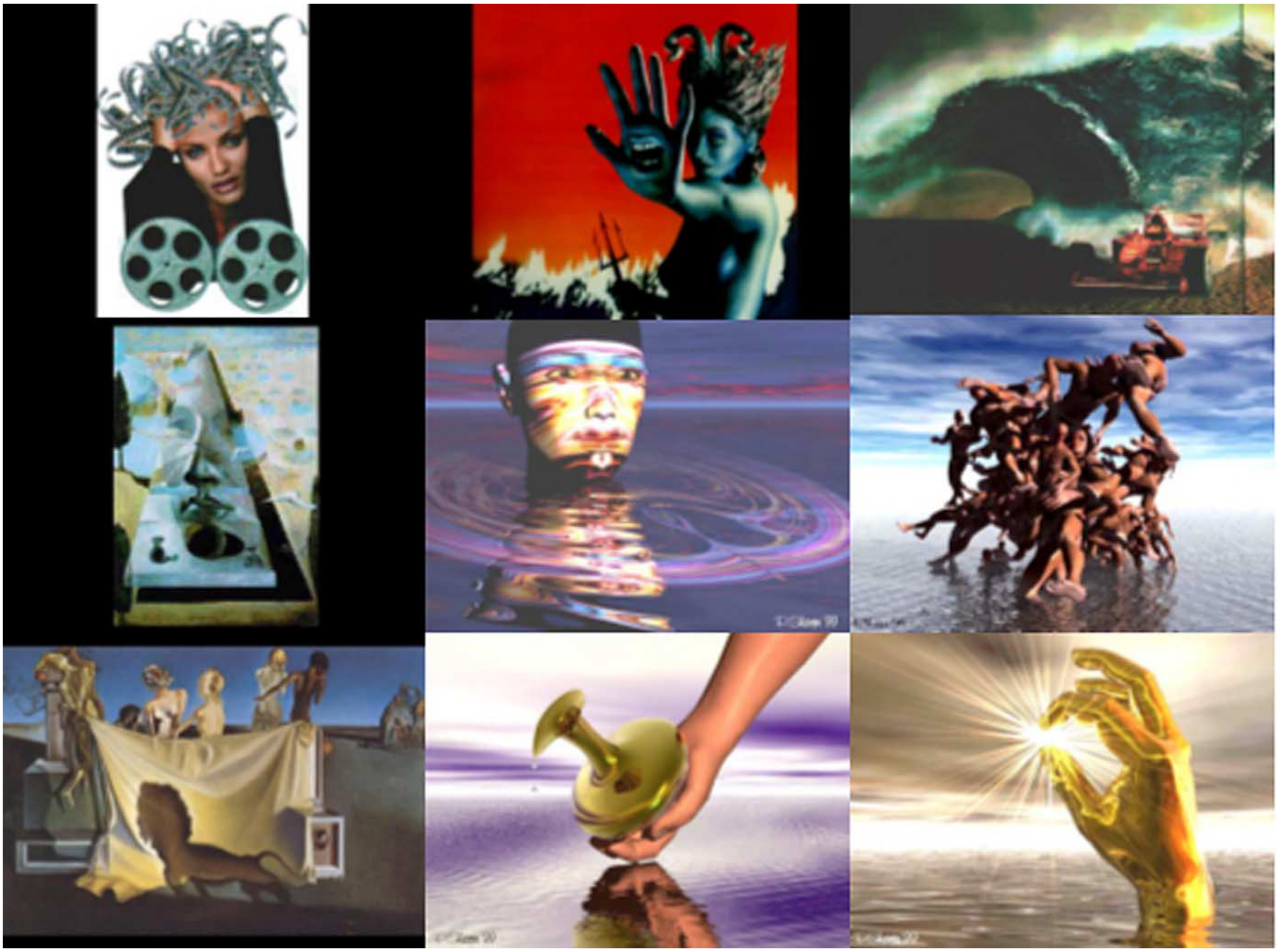
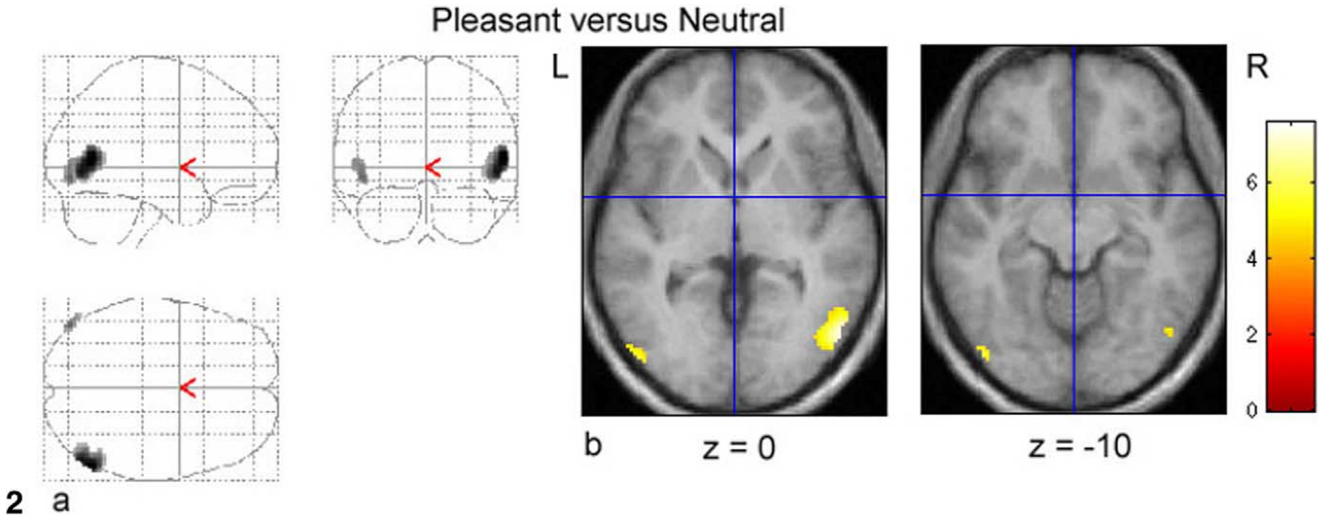


Fig. 1. Examples of "interesting" pictures.

Data analysis

Data were analyzed by using SPM99 (Wellcome Department of Cognitive Neurology, London, UK). All the scans were transformed into a standard space (Talairach and Tournoux, 1988) and smoothed in space using an 8-mm Gaussian filter (FWHM). All volumes were realigned to the first scan and residual motion effects were eliminated at each voxel by regressing a periodic function of the estimated movement parameters at each voxel on the time course of this voxel. The effects of the experimental conditions on the response variable were modeled as box-car functions smoothed with a hemodynamic impulse response and used as regressors in a general linear model (Friston et al., 1995). The statistical model included global and low frequency confounds. Predetermined contrasts of the condition effects were assessed at each voxel in a fixed-effects manner.

Additional analyses were performed on a set of regions of interest (ROIs). ROIs were defined by a conjunction of anatomical and functional information. The anatomical regions we focused on included the inferior occipital (MNI coordinates: left: −28, −82, −16; right: 28, −82, −14), middle occipital (left: −28, −92, 14; right: 32, −82, 14), and fusiform gyri (left: −34, −78, −18; right: 34, −78, −16), all of which have been shown to evoke strong responses to objects and scenes in the past. The middle temporal gyrus (left: −50, −70, 8; right: 48, −66, 10), which elicited robust responses in our experiment, was also included as an ROI. We also investigated an ROI situated on the posterior calcarine fissure (V1/V2; left: −8, −98, 2; right: 10, −96, 2). For each anatomically defined ROI, we averaged all voxels around the peak voxel within a 6-mm radius sphere that exhibited stronger responses to pictures from all categories compared to fixation (at a $P < 10^{-5}$) to create a representative time series for that ROI. Thus, for this analysis, the contrast of pictures vs fixation provided an unbiased functional selection criterion. Subjects' responses to neutral, pleasant, interesting, and unpleasant pictures were then defined, for each ROI, as a percentage increase relative to fixation and compared via repeated-measures ANOVAs. The statistical threshold for significance employed for the ROI analysis was a P value of 0.05.



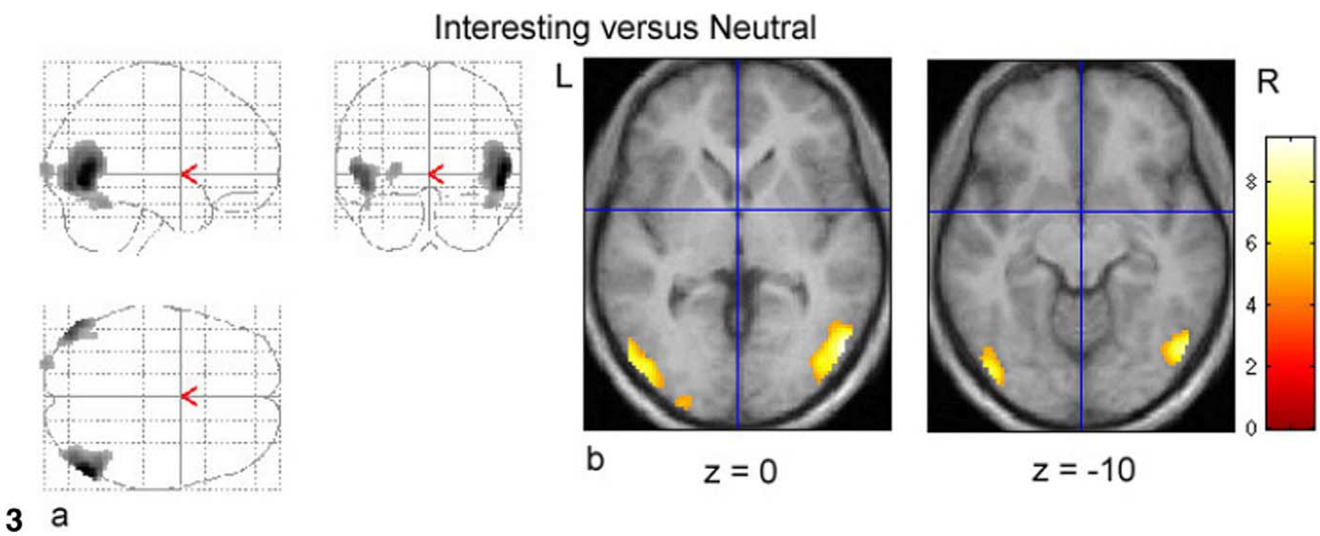


Fig. 2. Contrast of pleasant and neutral pictures. (a) Glass brains. (b) Axial slices at different *z* levels. Activations are displayed on an average group structural scan. The statistical threshold employed was a *P* value of 0.05 (corrected). The foci of activation and the associated *z* value are given in Table 1. The color bar indicates *z* values.

Fig. 3. Contrast of interesting and neutral pictures. (a) Glass brains. (b) Axial slices at different *z* levels. Conventions as in the legend to Fig. 2.

Results

Behavioral results

The ratings of the pictures revealed a main effect of valence [$F(3, 92) = 132.8$, $P < 0.001$]. Valence ratings of pleasant pictures were significantly higher and valence ratings of unpleasant pictures were significantly lower than valence ratings of interesting and neutral pictures. Subjects rated interesting and neutral sets as having equivalent degree of valence. Additionally, there was a main effect of arousal [$F(3, 92) = 77.0$, $P < 0.001$]. Arousal ratings were significantly higher for unpleasant and interesting pictures than for pleasant and neutral ones. Note that relatively low levels of arousal ratings for pleasant pictures were expected because erotic pictures were not included in our sample (see Lang et al., 1999). Interesting and pleasant pictures differed significantly in arousal level. Finally, arousal ratings for unpleasant pictures were significantly higher than for interesting ones. These results are summarized in Table 1.

Table 1
Mean valence and arousal ratings (standard deviation values are given in parentheses)

	Unpleasant	Pleasant	Neutral	Interesting
Valence	2.37 (0.83)	7.25 (0.72)	5.47 (0.91)	5.42 (0.99)
Arousal	7.40 (0.73)	3.69 (1.14)	3.85 (0.82)	5.73 (0.97)

Imaging results

Initially, we contrasted pleasant and neutral pictures (Fig. 2). Because these two categories did not differ in arousal level, their contrast reveals differential activity due to stimulus valence. Greater activity due to pleasant pictures was observed in occipitotemporal visual processing regions, including the inferior and middle occipital gyri and the middle temporal gyrus (the latter two regions appeared stronger on the right; but see below). We also observed differential activation in the left amygdala. For Talairach coordinates and cluster sizes, see Table 2.

Next, we contrasted interesting and neutral pictures (Fig. 3). Because these two categories did not differ in valence level, their contrast reveals differential activity due to stimulus *arousal*. In this case, we observed activations in the inferior and middle occipital gyri, the fusiform gyrus, and the middle temporal gyrus. We also observed differential activation in the left amygdala for $P < 0.01$ (uncorrected).

We also contrasted activation due to unpleasant pictures with those by neutral pictures. We observed differential activity evoked by unpleasant pictures in several visual regions, including the inferior occipital gyrus, the middle occipital gyrus, the fusiform gyrus, and the middle temporal gyrus. The left amygdala was also more strongly activated by unpleasant pictures.

Finally, we contrasted unpleasant and interesting pictures. Although pictures from both categories had high arousal, as stated above, unpleasant pictures had, on average, higher arousal levels. This contrast produced no differential activity at the standard threshold of $P = 0.001$ (uncorrected). Nevertheless, at a more lenient threshold of $P = 0.01$, we observed differential activation in the right lingual gyrus posteriorly, bilateral inferior occipital gyrus, as well as in the fusiform gyrus bilaterally. For the opposite contrast, namely regions exhibiting greater activation for interesting compared to unpleasant pictures, we only observed a small focus of activation in the anterior cingulate cortex.

The above voxelwise results were complemented by an additional region of interest (ROI) analysis. Because our study was aimed at probing visual activation during emotional perception, we focused our analysis on visual areas within the occipitotemporal cortex, including regions that have been shown in the past to elicit strong responses to images containing objects, faces, and scenes. Accordingly, we created bilateral ROIs for the inferior occipital gyrus (IOG), middle occipital gyrus (MOG), and fusiform gyrus (FG). The middle temporal gyrus (MTG) elicited robust responses in our experiment and was also included as an ROI. We also included a region along the posterior calcarine fissure (V1/V2). For each ROI, we tested for condition and hemisphere effects. Because we found no statistically significant effects of hemisphere or significant condition by hemisphere interactions, the results from the left and right hemisphere were combined. As in our voxelwise analysis, we were interested in the contrast of pleasant and neutral pictures so as to probe for valence-related activations, and the contrast of interesting and neutral pictures so as to probe for arousal-related activations. Pleasant pictures evoked greater activation than neutral ones in the IOG ($P < 0.05$), FG ($P < 0.05$), and MTG ($P < 0.001$). Interesting pictures evoked greater activation than neutral ones in the IOG ($P < 0.001$), MOG ($P < 0.05$), FG ($P < 0.005$), and MTG ($P < 0.0005$). Moreover, unpleasant pictures evoked greater activation than interesting ones in the IOG ($P < 0.001$) and

Table 2
Regions activated in the contrast of Pleasant versus Neutral, Unpleasant versus Neutral, and Interesting versus Neutral

Area	Coordinates (*x,y,z*)	*T* (*z* score)
Pleasant versus Neutral		
Inferior occipital gyrus		
Right	52, −72, −4	7.14
Left	−48, −82, 0	5.51
Middle occipital gyrus (right)	56, −64, 8	7.55
Middle temporal gyrus (right)	54, −58, 5	5.54
Amygdala (left)	−18, −8, −14	3.86
Anterior cingulate	0, 16, −2	3.84
Interesting versus Neutral		
Inferior occipital gyrus		
Right	32, −92, 2	3.69
Left	−38, −90, 2	4.79
Middle occipital gyrus		
Right	46, −76, 12	6.72
Left	−54, −76, 2	7.43
Middle temporal gyrus		
Right	56, −68, 4	9.07
Fusiform gyrus		
Right	46, −56, −22	5.7
Left	−46, −64, −24	4.98
Intraparietal sulcus		
Right	30, −78, 30	4.29
Amygdala* (Left)	−24, −6, −30	2.35
Unpleasant versus Neutral		
Inferior occipital gyrus (posterior)		
Left	−28, −98, 2	5.88
Inferior occipital gyrus (anterior)		
Right	38, −82, −18	6.39
Left	−38, −82, −14	7.08
Middle occipital gyrus		
Right	38, −90, 2	5.16
Left	−36, −90, 2	5.11
Fusiform gyrus		
Right	46, −60, −22	7.53
Left	−48, −68, −16	7.85
Middle temporal gyrus		
Right	54, −62, 8	7.32
Left	−54, −64, 8	5.19
Intraparietal sulcus (Right)	30, −78, 34	4.33
Amygdala (Left)	−20, −4, −24	3.66
Anterior insula (Right)	48, 20, −12	3.76
Midbrain (Right)	8, −26, −8	4.98
Thalamus (Right)	0, −14, 4	3.84
Frontal pole	0, 52, 30	3.63
Middle frontal gyrus	56, 22, 32	4.21

Note. Activations are all significant at $P < 0.001$ (uncorrected), except when indicated by an asterisk ($P < 0.01$).

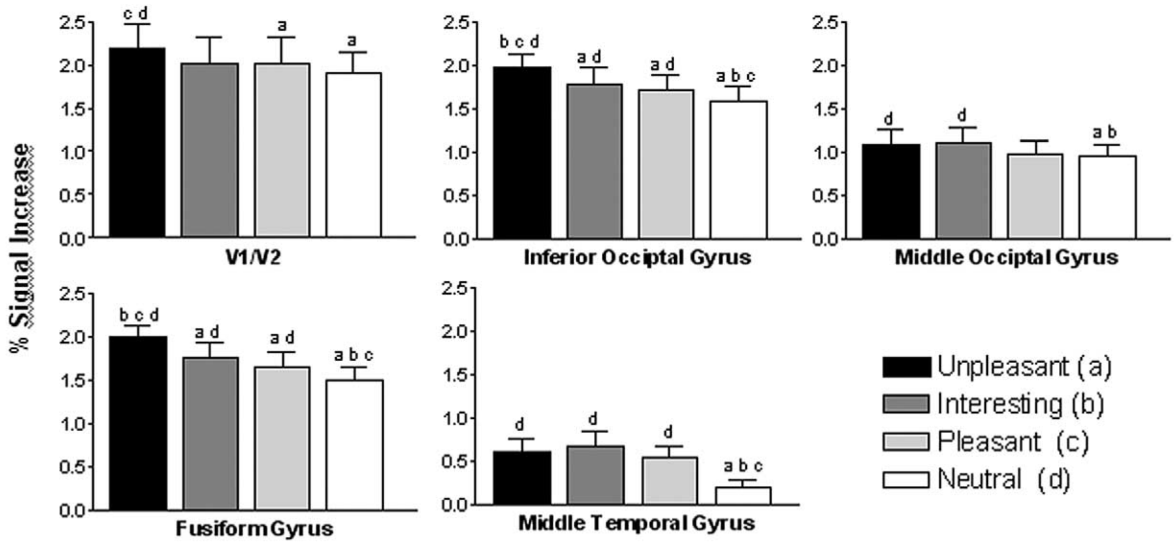


Fig. 4. Region of interest (ROI) analysis. For each ROI, response strength is indicated in terms of percentage increase relative to fixation trials. Results from the left and right hemispheres did not differ and were pooled. The letters above the error bars indicate the conditions that differed significantly from that specific condition (see condition labels) according to post hoc tests (see text for specific P values).

FG ($P < 0.005$). Finally, unpleasant pictures evoked greater responses in V1/V2 compared to both pleasant ($P < 0.05$) and neutral ($P < 0.01$) pictures. The complete pattern of results is shown in Fig. 4.

Discussion

The present study showed increased visual activation during emotional perception relative to viewing neutral pictures, consistent with previous findings (Lang et al., 1998; Lane et al., 1997a, 1997b, 1999; Taylor et al., 1998, 2000; Breiter et al., 1996; Moll et al., 2002a; Morris et al., 1998; Vuilleumier et al., 2001; Rotshtein et al., 2001; Pessoa et al., 2002a). For example, Lang et al. (1998) investigated the activation of visual cortex when subjects viewed emotional and neutral pictures. Whereas both emotional and neutral pictures produced activity within and around the calcarine fissure (V1/V2), only emotional pictures also produced sizable clusters of activity bilaterally in the occipital gyrus (BA 18/19), and in the right fusiform gyrus. Lane et al. (1999) also obtained evidence for differential activation in visual cortex depending on the category of the stimulus seen by subjects. In particular, both pleasant and unpleasant stimuli activated extrastriate visual cortex (BA 18/19) bilaterally when compared to neutral stimuli. Moreover, the right anterior temporal cortex was also more active when emotional pictures were compared to neutral pictures. In another study, Taylor et al. (2000) studied the effect of stimulus unpleasantness on visual activation. They compared visual activation for nonaversive, mildly aversive, and strongly aversive pictures. They found a stepwise increase in activation in visual cortex associated with increasing aversive picture content. Comparison of aversive and nonaversive stimuli revealed differential activity in posterior visual regions, including the lingual gyrus, the middle occipital gyrus, as well as the fusiform gyrus and the middle temporal gyrus. Finally, in a recent study, Pessoa et al. (2002a) have obtained evidence that very early visual areas within and surrounding the calcarine fissure (V1/V2) are also modulated by valence. The results from these and other studies demonstrate that, compared to viewing neutral pictures, viewing emotional pictures is associated with greater visual activation throughout occipitotemporal cortex.

The studies discussed above did not compare experimental conditions that were explicitly controlled for arousal level. In fact, in many cases the comparisons involved emotional and neutral conditions, which are typically associated with large differences in arousal level. Therefore, the increased visual activation associated with emotionally charged stimuli might have had little to do with the valence of the pictures per se. Instead, the main determinant of visual activation may have been the arousal level of the pictures. In fact, Bradley et al. (2003) recently showed that activity in visual areas is linked to subjective arousal ratings.

In the present study, to investigate the contributions of valence and arousal to visual activation, we compared conditions matched in arousal, revealing contributions of valence, and conditions matched in valence, revealing contributions of arousal. The contrast of pleasant and neutral pictures revealed differential activity for pleasant pictures in visual cortex. Because the two conditions were matched in terms of arousal (average ratings of 3.69 and 3.85, respectively), but differed in valence (average ratings of 7.25 and 5.47, respectively), the contrast reveals valence-related contributions to visual cortical activation. We also created a new category of “interesting” stimuli designed to have high arousal, but neutral valence. The comparison of interesting and neutral pictures revealed differential activation throughout large portions of visual cortex. Because the two conditions were matched in terms of stimulus valence (average ratings of 5.42 and 5.47, respectively), but differed in arousal level (average ratings of 5.73 and 3.85, respectively), this contrast demonstrates that differences in valence are *not* necessary for differential visual activation. Moreover, this contrast also shows that differences in arousal are *sufficient* to produce visual activation. In our study, a major focus of activation included the so-called lateral occipital complex, a set of cortical regions known to be involved in the processing of objects and proposed to be an intermediate stage in the visual processing hierarchy (e.g., Lerner et al., 2002).

The voxelwise contrast of unpleasant and interesting pictures (corrected for multiple comparisons) did not reveal strong differential visual activation, even though there was a significant difference in valence between the two conditions (average ratings of 2.37 and 5.42, respectively) and a small but significant difference in arousal level (average ratings of 7.40 and 5.73, respectively). However, differential activation for unpleasant relative to interesting pictures was revealed by our ROI analysis in the inferior occipital gyrus and fusiform gyrus. Although the differences were small in absolute magnitude, they were statistically significant. Consistent with such ROI results, when the threshold for significance was made less exacting, differential activation was observed in visual cortex in the statistical maps. It is noteworthy that the contrast of unpleasant vs neutral pictures revealed differential activation in subcortical structures, including right midbrain and right thalamus. Because these activations were not observed in other contrasts, they may reveal responses specific to unpleasant stimuli. In this context, Morris et al. (1999) showed that both the superior colliculus and the pulvinar showed increased "coupling" with the amygdala when subjects viewed briefly presented fear-conditioned faces that were presumably undetected by the subjects. Finally, the contrast of unpleasant vs neutral pictures also revealed differential in the posterior calcarine fissure (V1/V2) ROI, a finding consistent with previous results (e.g., Pessoa et al., 2002a) and the idea that the earliest stages of visual processing are modulated by emotional content (Pessoa et al., 2002b).

Our results demonstrate that both valence and arousal contribute to stronger visual cortical activation. Several brain systems contribute to arousal, including multiple brain stem nuclei, the nucleus basalis of Meynert in the basal forebrain, and the anterior cingulate cortex (Critchley et al., 2000). We found no evidence, however, that these structures were more heavily engaged by pictures with higher arousal levels, namely unpleasant and interesting pictures. However, basal forebrain regions typically have a low signal–noise relationship in fMRI, which may have precluded the observation of differential activation in these brain regions. The anterior cingulate region, on the other hand, has been activated by many cognitive tasks involving directed attention, executive processing, or explicit decision-making (Bush et al., 2000). In contrast, our study design did not require subjects to produce overt responses, allowing us to probe "spontaneous" brain responses to emotional and neutral stimuli that were uncontaminated by explicit executive processing, which may account for the absence of anterior cingulate activation in the contrast of unpleasant vs neutral and interesting vs neutral conditions.

In comparing different picture categories, it is important to discuss the possibility that other factors besides valence and arousal may have contributed to differential visual activation. In a recent study, Rothstein et al. (2001) compared regular faces to "expressional transfiguration" (ET) faces in which the eyes and mouth were inverted. These conditions were associated with similar levels of activation in visual cortex, although they produced different levels of adaptation (i.e., decreases due to stimulus repetition were greater for regular faces). ET faces were rated as highly bizarre, raising the possibility that stimulus bizarreness led to differential visual activation. However, subjects' ratings of bizarreness and unpleasantness (i.e., valence) were highly correlated ($r = 0.9$), making it difficult to parse the contributions of these distinct factors. In our study, the category of interesting pictures included many surreal images and, in a separate behavioral session, 50% of these pictures were rated as having moderate or high surreal content compared to 5% of the other categories. Because half of the interesting pictures were rated as having low or no surreal content, we believe that interesting pictures contributed to visual activation (compared to neutral) because of their higher arousal levels and not solely due to surreal content (or bizarreness). Subjects also rated the pictures in terms of clarity, which was found to be similar for interesting and IAPS pictures. Thus, it is unlikely that stimulus clarity provided a significant contribution to differential visual activation. Nevertheless, it is conceivable that differences in visual features (e.g., visual complexity) may have contributed to differential activation in the present study.

Attention is another potential source of differential visual activation. In the context of emotional perception, Lane et al. (1999) showed that both stimulus valence and attention modulate responses in extrastriate visual cortex (BA 18). Although in the present study subjects viewed images passively, it is possible that certain pictures, such as highly arousing unpleasant or interesting ones, "automatically" engaged more attention. Differences in attention are almost invariably associated with robust activations throughout a frontoparietal "attention network," whose main nodes include the frontal eye field (FEF), the supplementary eye field (SEF), the intraparietal sulcus (IPS), and the superior parietal lobule (SPL; Kastner and Ungerleider, 2000). In the present study, for the contrasts of pleasant and neutral pictures and for the contrast of interesting and neutral pictures, only very limited differential activation was observed in nodes of the attentional network. Critically, activations were restricted to a single site (either the anterior cingulate or the anterior IPS) and were not distributed throughout the attention network, as nearly always is the case (Kastner and Ungerleider, 2000; Corbetta and Shulman, 2002; Pessoa et al., 2002b, 2003). Thus, although the contributions of attention cannot be completely ruled out, we believe that such effects, if present, were quite small.

Finally, because eye movements were not monitored during the scans and because pictures were displayed for 5 s, differential eye movements produced while images were being viewed may also have contributed to the differential visual activation we observed. It has been shown, however, that emotional and neutral pictures of the IAPS database are not associated with differential eye movements (Lang et al., 1998; Lane et al., 1999). In general, eye movements reliably engage a network of brain regions that includes the FEF, the SEF, the IPS, and the SPL. As the work of Corbetta and colleagues has shown (1998; see also Beauchamp et al., 2001), the "eye-movement network" largely overlaps with the "spatial attention network." Critically, in the contrasts of pleasant vs neutral and interesting vs neutral, the only indication for activation of this network was a very small focus of activation in the posterior IPS. Thus, we believe that the contributions of eye movements, like the contribution of attention, were very small, if any.

In summary, the present study provides evidence that *both* stimulus valence and arousal level contribute to visual activation during emotional perception. Further studies in which parametric variations of valence and arousal are used may further clarify the differential contributions of these two sources of visual activation during emotional perception.

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