Influence of attentional demands on the processing of emotional facial expressions in the amygdala

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Recent studies have cast doubts on the appealing idea that the processing of threat-related stimuli in the amygdala is unconstrained by the availability of attentional resources. However, these studies exclusively used face stimuli presented at fixation and it is unclear whether their conclusion can apply to peripheral face stimuli. Thus, we designed an experiment in which we manipulated the perceptual attentional load of the task used to divert attention from peripheral face stimuli: participants were presented simultaneously with four peripheral pictures (two faces, either both neutral or both fearful, and two houses) that were slightly tilted, and had to match two of these pictures (defined by their position on the screen) either for orientation of the tilt or for identity. The identity task was confirmed to involve greater attentional load than the orientation task by differences in accuracy, reaction times, subsequent face recognition performance, and patterns of activation in several cortical regions. In the orientation task, ignored fearful faces led to stronger activation in the right amygdala than ignored neutral faces. However, this differential response was abolished when participants performed the difficult identity-matching task. Thus, emotional processing of peripheral faces in the amygdala also appears to depend on the available perceptual attentional resources.
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Keywords: Amygdala; Attentional load; Emotion; Fear; fMRI

During the last decades, evidence has accumulated suggesting that emotional events, and especially threatening ones, can be encoded automatically, i.e., involuntarily and independently of attentional resources (see Compton, 2003, for a review). This particular processing presents obvious adaptive advantages: it would allow attention to be drawn quickly to emotional stimuli, which in consequence would receive priority for processing. The amygdala, a subcortical structure strongly involved in the emotional processing of sensory stimuli (see Zald, 2003; Phelps and Ledoux, 2005, for reviews), is thought to play an essential role in this phenomenon (e.g., Öhman, 2005; Vuilleumier, 2005). The amygdala could perform a rapid, though crude, evaluation of the emotional value of incoming stimuli, based on inputs from low-level sensory cortices as well as from sub-cortical sites (Adolphs, 2002), and supply direct and indirect top–down signals to sensory pathways, which can modulate the representation of emotional stimuli (Anderson and Phelps, 2001; Pessoa and Ungerleider, 2004; Vuilleumier, 2005; Phelps, 2006).

In line with this view, several studies have shown that responses to threatening stimuli (mainly fearful faces) in the amygdala can be observed when these stimuli are presented outside the focus of attention. Vuilleumier et al. (2001) designed an experiment in which participants were presented with brief visual displays containing two faces and two houses arranged in vertical and horizontal pairs at eccentric locations. The two faces either both had a neutral expression or both had a fearful expression. Participants were required to attend selectively to either the vertical or the horizontal pair of stimuli, while maintaining central fixation, in order to perform a same/different matching judgment for these two stimuli. The results revealed larger amygdala activation for fearful faces than for neutral faces regardless of the initial allocation of spatial attention (see also Vuilleumier et al., 2004). Likewise, differential amygdala activation has been reported by Anderson et al. (2003) using semi-transparent pictures of either fearful or neutral faces superimposed on pictures of places, when participants made a male/female judgment (i.e., attended to the faces), but also when they made a inside/outside judgment (i.e., attended to the places and ignored the faces). More recently, similar results have been obtained also by Williams et al. (2005) in a more difficult task, with pairs of composite face/place stimuli (of the same kind as those used by Anderson et al., 2003), presented simultaneously on either side of a central fixation point.

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 Available online on ScienceDirect (www.sciencedirect.com).

The participants had to perform a same/different judgment either on the faces or on the places, and in either case, amygdala activation differed for neutral and fearful faces. Altogether, these results are consistent with the view that the processing of threat-related stimuli in the amygdala is unconstrained by the availability of attentional resources.

However, evidence for suppression of differential amygdala response to fearful and neutral faces under condition of inattention is also present in the literature. When participants are instructed to match for orientation two small bars presented in the peripheral visual field, while at the same time ignoring neutral and fearful faces presented at fixation, the enhanced amygdala activation to fearful faces vanishes (Pessoa et al., 2002).

These discrepant results may be explained by differences in the perceptual attentional demands of the tasks used to divert attentional resources from the faces (Bishop et al., 2007; Pessoa et al., 2002, 2005; Williams et al., 2005). According to Lavie (1995, 2000, 2005), when attention is focussed on a task at hand, the processing of task-irrelevant stimuli would be prevented when the processing of task-relevant stimuli places very high demands on the perceptual system. However, if the processing of task-relevant stimuli does not exhaust all the available capacity, any spare capacity would "spill over" to the processing task-irrelevant stimuli. In other words, the amount of task-irrelevant processing that takes place is dependent on the perceptual attentional load. Irrelevant information processing could occur under conditions of low attentional load, but would be eliminated by high attentional load. Using this framework, positive results (Vuilleumier et al., 2001; Anderson et al., 2003; Williams et al., 2005) could arise from the fact that the tasks used to divert attention from the faces were always less attention-consuming than the peripheral bar-orientation task designed by Pessoa et al. (2002).

Pessoa et al. (2005) performed a direct test of this "differential load hypothesis". They used the same task as in their previous study (Pessoa et al., 2002), but created three levels of attentional load (low, medium, and high, within subjects) by varying the angular difference of the bars. They reported differential amygdala activation for unattended neutral and fearful faces at fixation only during the low-load condition, and an absence of emotion-related responses in the medium-load and high-load conditions. Consistent results have also been reported for participants performing a letter search task of high or low perceptual attentional load superimposed on fearful or neutral faces: differential amygdala activation to faces was either observed only during the low-load task (Bishop et al., 2007), or eliminated for both levels of load (Mitchell et al., 2007). Attentional load therefore appeared to be an important determinant of the extent of amygdala engagement by task-irrelevant stimuli. However, at least some of the tasks leading to differential amygdala activation for fearful and neutral faces have been argued to involve high perceptual attentional load (Williams et al., 2005).

The spatial positioning of the to-be-ignored stimuli in the visual field could be considered as another important factor explaining the discrepancies. Indeed, the pattern of results to date suggests that unattended fearful faces presented at fixation may only trigger amygdala responses under low-load but not high-load conditions (Anderson et al., 2003; Bishop et al., 2007; Pessoa et al., 2002, 2005), whereas unattended fearful faces presented in the periphery may activate the amygdala under both low (Vuilleumier et al., 2001, 2004) and high (Williams et al., 2005) attentional-load conditions. It has been shown the incidental emotional processing in the amygdala relies on coarse visual information represented in the low spatial frequencies of the images (Vuilleumier et al., 2003; Winston et al., 2003), conveyed by the magnocellular visual pathway. Since this pathway is driven maximally by inputs from the visual periphery (Kandel et al., 2000; Livingstone and Hubel, 1987), the amygdala may be especially sensitive to peripheral faces, consistent with the idea that this structure plays an important role in *directing* the attentional focus to emotionally relevant stimuli in the visual field.

Also, as underlined by Lavie (1995, 2000), the perceptual attentional-load model relies almost entirely on evidence from peripheral distractors, leaving open the possibility that ignoring stimuli at fixation may involve different mechanisms (Beck and Lavie, 2005). Different/higher levels of cognitive control and *active* suppression of amygdala responses may be involved in order to limit the interference caused by irrelevant faces at fixation (Mitchell et al., 2007; Ochsner and Gross, 2005; Pessoa et al., 2005). Moreover, face stimuli may have a special status with regard to the attentional-load model, due to their biological and social significance (Lavie et al., 2003). Behavioural experiments indicate that, even if face processing is probably not entirely capacity free, interference from irrelevant distractor faces presented in the periphery may not depend on the extent to which the relevant task loads attentional capacities (Lavie et al., 2003). Therefore, studies showing that differential amygdala responses to neutral and fearful faces presented at fixation depend on the available attentional resources (Bishop et al., 2007; Pessoa et al., 2002, 2005) cannot guarantee that the same results will stand out for faces presented in the periphery.

In order to test whether the processing of peripheral face stimuli can be influenced by attention under high perceptual load conditions, we designed a functional magnetic resonance imaging (fMRI) experiment using peripheral stimuli in which it was possible to manipulate and quantify the effects of attentional load within participants. The same participants performed two attentional tasks of varying difficulty on peripheral stimuli, using exactly the same visual displays. Four pictures (two faces and two houses) were presented at the corners of an imaginary square centred on a fixation cross. All pictures were tilted slightly clockwise or anticlockwise, and in different blocks, participants matched two of the pictures (along one diagonal) either for orientation (easy, low-load task) or for identity (hard, high-load task). The pictures to be matched were always two faces expressing the same emotion (neutral or fearful) or two houses. In order to confirm the effects of this attentional manipulation on performance, we first ran a behavioural version of this experiment, where we also measured the differential effects of the two attentional tasks on subsequent face recognition. The validity of the attentional manipulation was further substantiated by the examination of attention-related modulations of activation in functionally specialised cortical areas that respond preferentially to faces (Allison et al., 1994; Puce et al., 1996, 1998; Kanwisher et al., 1997; Wojciulik et al., 1998; Haxby et al., 2000; Ishai et al., 2000; Narumoto et al., 2001; Vuilleumier et al., 2001; Anderson et al., 2003; Williams et al., 2005; Vuilleumier and Pourtois, 2007) or places and scenes (Aguirre et al., 1996; Epstein and Kanwisher, 1998, Epstein et al., 1999).

Material and methods

Participants

Ten right-handed participants (3 males) aged 18–30 performed the behavioural experiment, and another fourteen right-handed

healthy volunteers (6 males) aged 19–35 took part in the main fMRI experiment. All had normal or corrected-to-normal vision and no history of neurological or psychiatric illness. The study was approved by the local ethics committee.

Stimuli

Ninety-six pictures of faces and 96 pictures of houses were used for this experiment. The face stimuli were built using GenHead V1.2, Academic Version (Genemation: The Face Creation Company, Manchester, www.genemation.com). Forty-eight different individual faces (24 males) with a neutral and a fearful expression were generated and edited. Pictures of houses were cropped to fit within an oval shape close to the overall shape of the face stimuli (3.5°×5°). The stimuli were presented as black-and-white displays on a black background. Mean luminance and contrast across the categories were equated.

Sixty-four four-picture displays were built, each using different face and house stimuli (see Fig. 1). Each display was made of two faces and two houses tilted 25° clockwise or anticlockwise. The four pictures were presented at the corners of an imaginary square centred on a white fixation cross (the angular distance from the centre of the fixation cross to the centre of each stimulus was 6.5°). The two pictures of one category were always presented along one diagonal of the imaginary square (i.e., upper left corner and lower right corner – D1, or upper right corner and lower left corner – D2). The two faces in one display always expressed the same emotion (either both neutral, or both fearful).

The following factors were fully balanced across the four-picture displays: position of the faces (D1/D2), expression of the faces (neutral/fearful), identity match (same/different) along D1 and D2, and orientation match (same/different) along D1 and D2. When two different faces were presented, they were of the same gender in half of the trials (balanced across the expression of the faces and the same/different orientation conditions). The four possible combinations of orientations used for each pair of stimuli occurred with the same probability along D1 and D2, and were balanced as much as possible across the different factors.

Behavioural experiment

Participants were required to perform two different tasks presented in a blocked design and in balanced order (see Fig. 1). In the orientation task (easy task/low load), they had to match two of the pictures of the four-picture display (along D1 or D2) for orientation, regardless of identity. In the identity task (hard task/ high load), they had two match the two pictures for identity, regardless of orientation. The other pictures of the displays were to be ignored. Within the orientation or identity tasks, the relevant locations on which to perform the matching task were blocked but the stimulus type appearing at these locations (faces or houses) was not. Thus, each task contained the following four experimental conditions in a randomized order: matching neutral faces (Attended Neutral, AN) or fearful faces (Attended Fearful, AF) at relevant locations (with houses presented at the irrelevant locations), or matching houses at relevant locations in the presence of neutral faces (Unattended Neutral, UN) or fearful faces (Unattended Fearful, UF) at irrelevant locations. Participants had to respond as quickly and as accurately as possible, by pressing one of two keys with the right hand (index finger: yes, middle finger: no). Each of the 64 four-picture displays was presented twice for each task (once for matching along D1, once for matching along D2). Thus, within each task, one given pair of stimuli appeared once at attended locations and once at unattended locations.

In the behavioural experiment, the identity and orientation tasks were further split in two parts, presented in balanced order. In one part, participants were only required to perform the orientation or identity task (single-task condition). In the other part, they also had to perform a face-recognition task (dual-task condition): for each four-picture display, after the participants had given their orientation/identity response, two faces were presented and the participants had to decide which of them had appeared in the preceding four-picture display. In half of the trials, the two faces displayed for the recognition task expressed the same emotion (either both neutral or both fearful), in the other half, the two faces expressed different emotions. This variable, as well as the position (left or right) of the face matching one of the faces of the preceding four-picture display, was balanced across the different attention conditions (AF, AN, UF and UN). The recognition task was presented as a secondary task and emphasis was put on accurate performance on the orientation/ identity task.

Thus, participants completed four different blocks of 64 trials: orientation single, orientation dual, identity single, identity dual. Each block started with an instruction screen presented for 5 s indicating which task had to be performed and which pictures (D1 or D2) had to be matched. After 32 trials, a new instruction screen prompted the participants to attend to the two other positions of the four-picture display. The order of presentation of the four-picture displays within each block was randomized between participants.

Each trial began with a white fixation cross displayed in the centre of the screen for 500 ms. Then, a four-picture display was presented for 250 ms, followed by a question mark for 2 s. In the single-task conditions, a white dot was then presented for 0 to 12 s (mean=4.6 s) before the onset of the next trial. The duration of the white dot was the same as for the fMRI experiment: it followed a
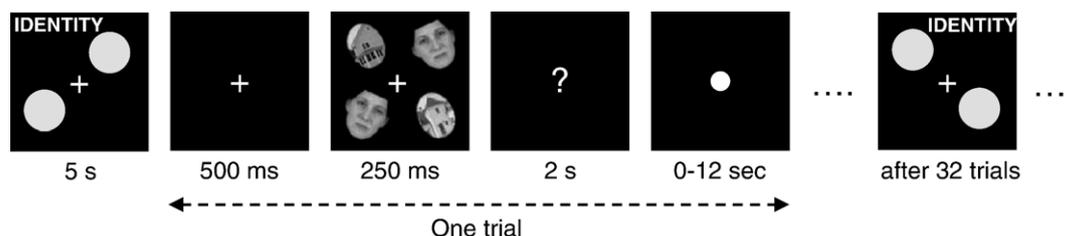

Fig. 1. Sequence of events in a typical trial of the behavioural experiment in the single-task condition (same as for the fMRI experiment). An instruction screen, indicating which task to perform (orientation or identity) and which pictures to match, appeared at the beginning of each run. After 32 trials, a new instruction screen prompted the participants to attend either to the same positions, or to the two other positions of the four-picture display.

logarithmic distribution skewed towards shorter durations (50% of the intervals lasted 0–3.9 s, 34.3% lasted 4–7.9 s, and 15.7% lasted 8–12 s), to enable the relative separation of haemodynamic responses of individual events within single trials (Friston et al., 1998; cf. Nobre et al., 2004), while keeping the task to an endurable length. In the dual-task conditions, the question mark was followed by the presentation of two faces of the same gender (one on each side of a centred fixation cross) for 1 s, then a question mark appeared for 2 s, followed by the white dot for 0 to 7 s (mean=1.6 s) before the onset of the next trial (although the dual tasks were not designed for imaging, this duration was also jittered to keep the single and dual tasks as similar as possible). Central fixation was required throughout, except during the face-recognition task.

fMRI experiment

The stimuli and the structure of the trials were the same as in the behavioural experiment. So was the procedure, but for one aspect: participants only performed the single orientation and identity tasks. These two tasks were completed in two different runs (order balanced) of 128 trials (32 trials for each of the AN, AF, UN and UF condition). Each task was divided into two sequences of attention directed to D1 and two sequences of attention directed to D2, using different ABAB, BABA, ABBA, or BAAB series across different participants.

In addition, participants had to perform a separate localizer task at the end of the experiment. They were shown pairs of neutral faces (NF), fearful faces (FF), houses (Hou) or checkerboard-like grid-stimuli (Grid) in a blocked fashion. Each stimulus was presented for 500 ms, with an interval of 1500 ms between the stimuli, and participants had to decide whether two stimuli in a pair matched and make a speeded-choice response. Each block contained 4 trials (8 stimuli, 16 s in total), and was repeated 6 times throughout the localizer task (with different stimuli for each block of faces and houses). The blocks were presented in a randomized order, separated by 6 s fixation, and were then followed by one baseline block (fixation cross presented for 16 s).

Image acquisition

Magnetic-resonance images were acquired using a Siemens Trio 3 T scanner equipped with a Siemens 8-channel head coil (127 MHz) at the Centre for Clinical agnetic Resonance Research of Oxford (OCMR), United Kingdom. Visual stimuli were presented on a translucent screen positioned at the rear-end bore of the magnet, using a projector placed outside the scanning room. Participants viewed the screen via an angled mirror placed above their head and gave responses using a custom-made MRI-compatible button box. Functional images were obtained with a single-shot T2*-weighted echo-planar imaging (EPI) sequence (TE=30 ms, TR=3.07 s, flip angle=90°). Fifty contiguous coronal slices with a thickness of 3 mm covered the whole brain but the frontal pole (64×64 matrix with a field of view of 19.2 cm, resulting in a voxel size of $3\times3\times3$ mm^3). An automated shimming algorithm was used to reduce magnetic field inhomogeneities (Wilson et al., 2002). The main experiment was conducted in two runs consisting of 327 images each (≈16.3 min each). The localizer task was performed in a separate run consisting of 205 images (≈9.8 min). The first 4 images of each run contained no experimental manipulation and were subsequently discarded to allow for T1 equilibration effects. A

structural image was acquired for each participant at the end of the session, using a high-resolution T1-weighted sequence (Inversion recovery-prepared 3D FLASH; TR=10 ms; TE=4 ms; flip angle=8° voxel size=$1\times1\times1$ mm^3).

Image processing and analysis

Data from the orientation task, the identity task and the localizer task were analysed separately off-line, using FSL (FMRIB Software Library, available at www.fmrib.ox.ac.uk/fsl). After the deletion of the first 4 volumes of each scan, images were corrected for the differences in the time of acquisition between slices and for head motion (applying rigid-body transformations with 6 degrees of freedom). Non-brain tissue was removed using BET (Brain Extraction Tool; Smith, 2002). High-resolution anatomical T1 images were co-registered with the realigned functional images, and structural and functional images were spatially normalized into a standardized anatomical framework (Montreal Neurological Institute 152-mean brain, contained within the FSL package). Functional data were spatially smoothed by a 6-mm full-width half-maximum Gaussian kernel and temporally high-pass filtered (with a cut-off at 128 s for the main tasks, and at 164 s for the localizer task). The time-series data were also corrected for temporal autocorrelation (Woolrich et al., 2001).

Data from individual participants were analyzed using a General Linear Model. The model included explanatory variables for the four experimental conditions of interest (AN, AF, UN, and UF) in each of the matching tasks (orientation and identity). The instruction screens were also modelled. Motion parameters from realignment corrections were entered as covariates of no interest. All the variables except for the motion parameters were modelled as extended events (including their duration) with a hemodynamic response function (gamma function, with a standard deviation of 3 s and a mean lag of 6 s). Group analyses used a mixed-effects model and a voxel-wise threshold of 2.32 ($p<.001$). Each cluster was corrected for multiple comparisons using Gaussian random theory as implemented in FSL, at the $p<.05$ level for the main tasks. The different contrasts were calculated using paired t tests. The localizer tasks were analyzed in a similar way. The explanatory variables were blocks of NF, FF, Hou, Grid, and baseline conditions; as well as the motion covariates. The correction for multiple comparisons was set at $p<.001$.

The main goal of this study was to investigate the effect of the attentional-load manipulation on amygdala responses to unattended neutral and fearful faces. To ascertain the reliability of our attentional-load manipulation, we defined regions of interest (ROIs) based on the localizer task (see Figs. 4 and 5). Regions of selective or preferential activation to faces were identified in the right lateral fusiform gyrus (FG) and right superior temporal sulcus (STS); whereas parahippocampal gyrus (PHG) regions were selectively responsive to places. For each participant, we created 12-mm-diameter spheres centred on the peak activation coordinates in the (NF+FF)–Grid contrast for the clusters found in the right FG (mean $x, y, z=43, -59, -20$) and the right STS (mean $x, y, z=48, -53, 10$), and in the Hou–Grid contrast for the cluster found in the right PHG (mean $x, y, z=28, -42, -15$). For one participant, no cluster was found in the STS and the sphere was centred on the mean coordinates derived from all other participants. Note that the clusters and peak locations obtained using this approach were very similar to those obtained with the (NF+FF)–Hou and Hou–(NF +FF) contrasts. The lower-level baselines were chosen in order to

lessen any possible distortions in the location of the activation peaks due to subtractions between nearby specialised areas.

Amygdala activations were investigated in both hemispheres using 10-mm-diameter spheres centred on the peak activation coordinates in the (FF–NF) contrast (right amygdala: $x, y, z = 26, -4, -18$; left amygdala: $x, y, z = -20, -4, -18, p < .05$ uncorrected). Because of the more variable nature of the signal in the area around the amygdala, it was not possible to identify regions of activation reliably across individuals. Therefore, ROIs were defined using the peak activation in the group analysis. We confirmed anatomically that the ROIs were located within the amygdala of all participants.

For each ROI, we computed the mean parameter estimates (averaged over all voxels within the ROI) for every single participant and each experimental condition (AN, AF, UN, and UF) within both orientation and identity matching tasks. We then converted these values into percent signal change, using the mean activity in the ROI over the whole time series as a baseline.

Results

Validation of the efficacy of the attentional-load manipulation was corroborated by behavioural data collected in the scanner as well as in an additional dual-task experiment, and by examining the levels of activation in brain areas selectively responsive to face or house stimuli. The central question of the study was addressed by comparing directly the difference between processing of unattended emotional versus neutral faces under conditions of high attentional load (identity task) and low attentional load (orientation task).

Behavioural data

Validation of attentional-load manipulation

Behavioural data were obtained from a behavioural experiment, in which a dual-task procedure enabled the direct measurement of explicit recognition of unattended face stimuli, as well as from the experiment conducted during fMRI scanning. Data from both experiments confirmed the efficacy of the attentional-load manipulation across the orientation and identity tasks.

In the behavioural experiment, the efficacy of the attentional-load manipulation was tested using 2×2 ANOVAs with task (orientation/identity) and attention (matching faces or houses) as within-subject factors.[1] Overall, participants were more accurate ($F(1,9) = 146.53, p < .001$) and faster ($F(1,9) = 40.86, p < .001$) in the orientation task than in the identity task (see Fig. 2). A main effect of attention also indicated that participants were more accurate when matching houses rather than faces ($F(1,9) = 24.64, p < .001$). However, this factor interacted with the task ($F(1,9) = 39.29, p < .001$), revealing that this was only true in the identity task ($F(1,9) = 33.90, p < .001$), consistent with the results of previous studies (Vuilleumier et al., 2001, 2004; Holmes et al., 2003). We also tested the effects of emotion (neutral/fearful) of unattended faces on accuracy and reaction times across the two tasks (orientation/identity), using 2×2 repeated-measures ANOVAs. No effect

involving the factor emotion reached significance, suggesting that, for both tasks, unattended fearful faces did not interfere more with performance than unattended neutral faces.

The behavioural data from the fMRI experiment replicated the significant difference in attentional load between the orientation and identity tasks (see Fig. 2). Main effects of task were obtained for both the accuracy ($F(1,13) = 163.90, p < .001$) and the reaction-time ($F(1,13) = 43.88, p < .001$) analyses, showing participants to be more accurate and faster in the orientation task compared to the identity task. The main effect of attention upon accuracy was also replicated ($F(1,13) = 28.62, p < .001$). An interaction between task and attention ($F(1,13) = 57.11, p < .001$) showed the performance advantage for matching houses was confined to the identity task ($t(13) = 6.74, p < .001$). Again, 2×2 repeated-measures ANOVAs testing the effects of emotion (neutral/fearful) of unattended faces on accuracy and reaction times across the two tasks (orientation/identity) revealed no effects involving the factor emotion.

Attentional modulation of emotional processing

Accuracy in the recognition task during the dual-task condition of the behavioural experiment (Fig. 3) provided a direct behavioural measure of residual resources for processing task-irrelevant face stimuli. Direct comparison of the explicit recognition of unattended faces of different emotions (fearful/neutral) in the two tasks (orientation/identity) showed a significant interaction ($F(1,9) = 6.07, p < .05$) between the two factors. Participants were more accurate for recognising fearful compared to neutral unattended faces in the orientation task ($t(9) = 3.94, p < .01$), but not in the identity task ($t(9) = 0.9, p > .92$). The accuracy for recognising unattended fearful faces was also higher in the orientation task compared to the identity task ($t(9) = 2.47, p < .05$). Recognition for unattended faces remained at chance level in all cases (all $p > .12$) except for fearful faces in the orientation task ($t(9) = 3.93, p < .01$). Interestingly, further follow-up analyses indicated that the improved recognition of unattended fearful faces in the orienting task only occurred when participants had to choose between two faces expressing different emotions during the recognition test (percent correct ± S.E. for unattended fearful faces: same emotion = $57.5 ± 5.33, p > .20$; different emotions = $78.75 ± 4.58, p < .001$). This suggests that, while performing the low-load orientation task on houses, residual attentional resources allowed only a very coarse processing of unattended faces, sufficient to extract the threatening information conveyed by these faces, but not to perceive their identity. As expected, attended faces were reliably recognised above chance level in both tasks (all $p < .001$).

Neuroimaging data

Validation of attentional-load manipulation

Direct validation for the attentional-load manipulation was also sought by comparing the effects of attention (match faces or houses) across the two tasks (orientation or identity) for both types of faces (neutral or fearful) in specialised cortical regions where attention-related modulations have been reported – the right FG, the right STS, and the right PHG (e.g., Wojciulik et al., 1998; O'Craven et al., 1999; Narumoto et al., 2001; Vuilleumier et al., 2004; Williams et al., 2005). Analyses using ROIs extracted based on the localiser task from individual participants gave qualitatively equivalent results as the whole-brain analysis.

Data extracted from individual ROIs in these areas (see Material and methods and Fig. 4) were analysed with $2 \times 2 \times 2$

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[1] The introduction of the recognition task did not modify significantly the behaviour of the participants in the primary orientation/identity tasks. Indeed, when accuracy and reaction times were analysed using a $2 \times 2 \times 2$ ANOVA with condition (single/dual), task (orientation/identity) and attention (matching faces or houses at relevant locations), no effect involving the condition (single/dual) factor reached significance (all F values < 1).
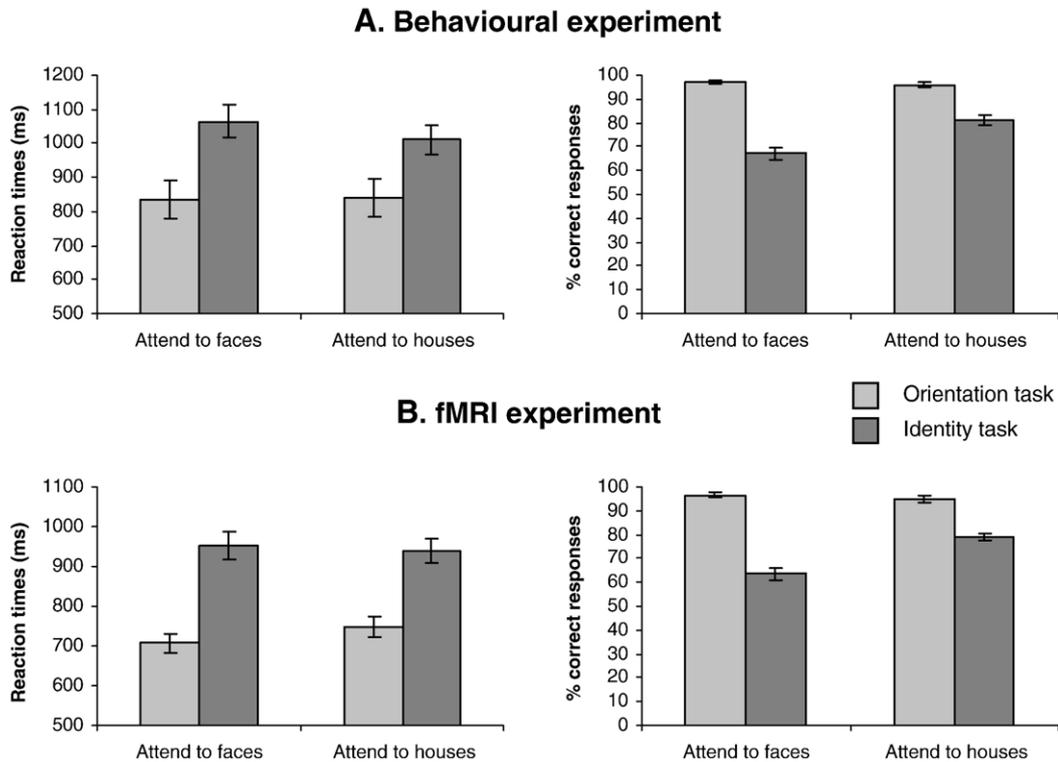
A. Behavioural experiment

B. fMRI experiment

Fig. 2. Reaction times (mean±S.E.) and percentages of correct responses (mean±S.E.) in the orientation task and in the identity task, when attending to faces or houses: (A) in the behavioural experiment; (B) in the fMRI experiment.

ANOVAs with task, attention, and emotion as within-subject factors. No effect involving the factor emotion reached significance. Activation in the FG was significantly greater when participants matched faces rather than houses ($F(1,13)=22.67$, $p<.001$). This effect was modulated by the task ($F(1,13)=10.83$, $p<.01$): the difference between the two conditions was larger in the identity task (mean difference±S.E.$=0.22\pm0.04$) than in the orientation task (0.10 ± 0.04). Similar results were obtained for the right STS, with greater activation when faces rather than houses appeared at attended locations ($F(1.13)=19.26$, $p<.001$), and greater attention-related modulations occurring in the identity task (mean difference±S.E.$=0.15\pm0.03$) than in the orientation task

Fig. 3. Recognition task: percentages of correct responses (±S.E.) in the orientation task and in the identity task for each experimental condition. AN=attended neutral faces; AF=attended fearful faces; UN=unattended neutral faces (attend to houses); UF=unattended fearful faces (attend to houses).

(0.06 ± 0.02) ($F(1,13)=11.94$, $p<.01$). Mirror results were found in the PHG, with greater activations when participants matched houses rather than faces ($F(1,13)=110.32$, $p<.001$). Again, this effect was modulated by the task ($F(1,13)=5.97$, $p<.05$), with a larger difference in the identity task (mean difference±S.E.$=0.28\pm0.03$) than in the orientation task (0.16 ± 0.03).

Attentional modulation of emotional processing in the amygdala

To begin with, the effects of emotion (neutral/fearful) of attended and unattended faces (match faces or houses) across the two tasks (orientation/identity) with different attentional loads were tested separately for the ROIs in the left and right amygdala, using $2\times2\times2$ repeated-measures ANOVAs. No effects were obtained in the left amygdala. The right amygdala was on average more activated by fearful faces than neutral faces ($F(1,13)=19.32$, $p<.001$) and when the participants attended to faces rather than houses ($F(1,13)=7.53$, $p<.05$). The interaction between the three factors did not reach significance ($F(1,13)=2.14$, $p=.16$). However, our main hypothesis was about the processing of *unattended* faces. Therefore, the effect of attentional load on the processing of unattended neutral and fearful faces was tested directly using 2×2 ANOVAs with task and emotion as within-subject factors for both amygdalae (see Fig. 5). Again, no effects were obtained in the left amygdala. A significant interaction between emotion and task ($F(1,13)=4.68$, $p<.05$) showed that there was significant emotion-related activation of the right amygdala by unattended fearful faces in the low-load orientation task ($t(13)=2.23$, $p<.05$) but not in the high-load identity task ($t(13)=0.2$, $p>.8$; the main effects were not significant). In line with previous findings, the right amygdala also showed greater activation for trials with attended emotional faces as compared to trials with attended neutral faces in both task
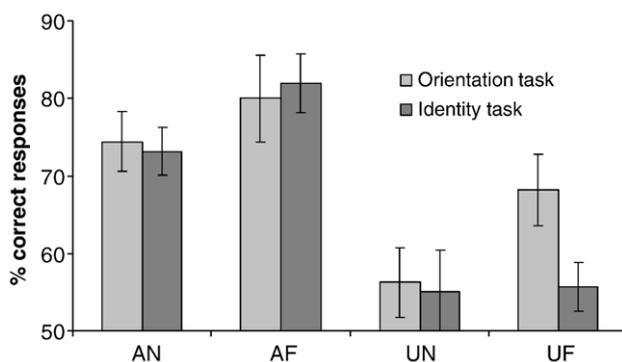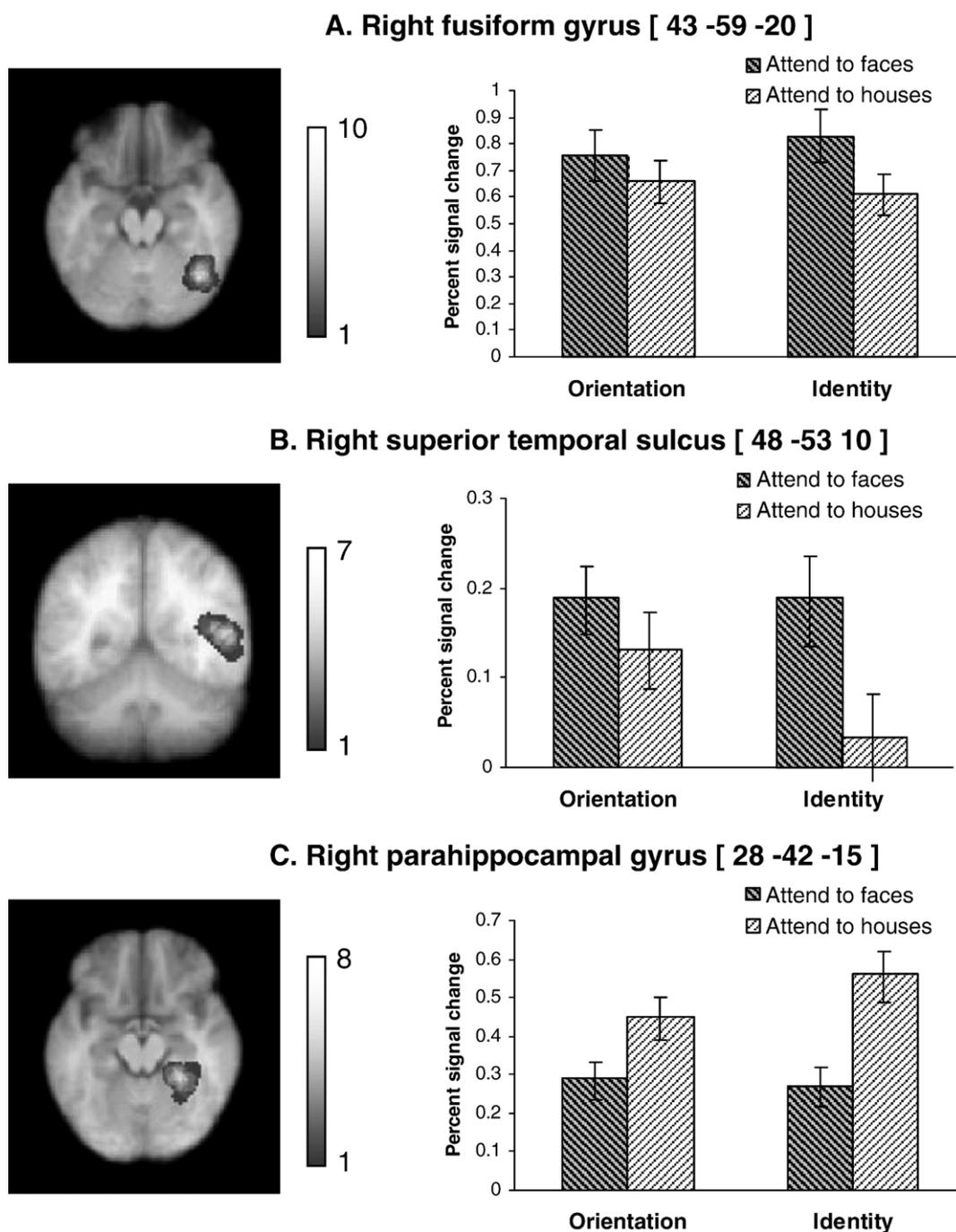
A. Right fusiform gyrus [43 -59 -20]

B. Right superior temporal sulcus [48 -53 10]

C. Right parahippocampal gyrus [28 -42 -15]

Fig. 4. For each of the cortical ROIs analysed, the mean percent signal changes (±S.E.) are shown when attention was directed to faces or houses in the orientation task and in the identity task (right panel). Individual ROIs (left panel) were superimposed over the 14 participants, with the brightness scale indicating the number of overlapping ROIs between participants.

conditions ($F(1,13)=26.5$, $p<.001$; orientation task: $t(13)=2.19$, $p<.05$; identity task: $t(13)=3.22$, $p<.01$; the main effect of task and the interaction were not significant).

Attentional modulation of emotional processing in cortical areas

To test whether the differential effects of unattended emotional faces under different attentional-load conditions was specific to the right amygdala, activations in the right FG, STS and PHG ROIs were also submitted to 2×2 ANOVAs testing the effects of emotion of unattended faces (neutral/fearful) and task (orientation/identity).

No region showed significant interactions between emotion and task or any main effects (all F values<1.6).

Discussion

The aim of this study was to test whether the differential response of the amygdala to peripheral emotional versus neutral faces is constrained by the attentional resources available for their processing. To this purpose, we designed an experiment in which
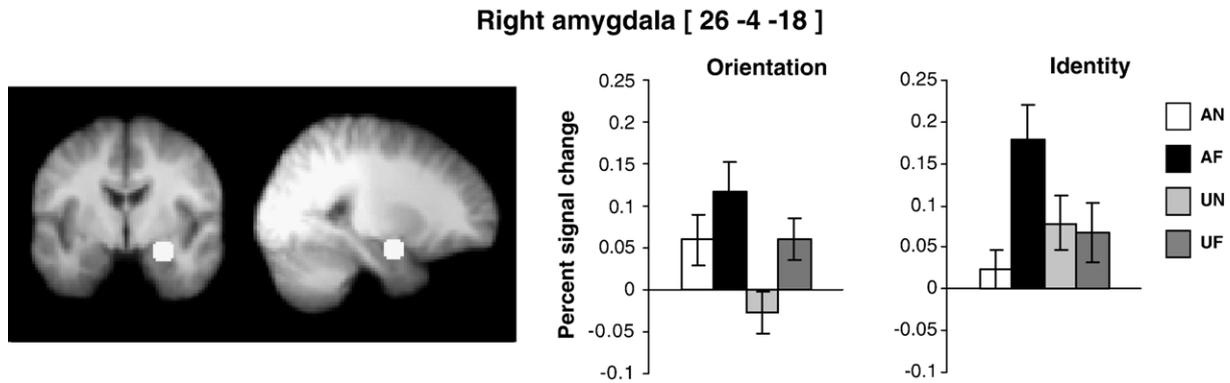
Right amygdala [26 -4 -18]

Fig. 5. Mean percent signal changes (±S.E.) in the right amygdala for attended neutral faces (AN), attended fearful faces (AF), unattended neutral faces (UN), and unattended fearful faces (UF) in the orientation task and in the identity task (right panel). The same ROI was used for all participants (left panel).

the difficulty of the task used to divert attention from face stimuli varied. The same participants were presented with visual displays made up of four peripheral pictures (two faces, either both neutral or both fearful, and two houses) that were slightly tilted, and were asked to match two of these pictures (defined by their position on the screen) either for orientation of the tilt or for identity. In both tasks, fearful faces led to larger right amygdala activation than neutral faces when they were presented at attended locations. The same pattern of result was found for unattended faces in the orientation/low attentional-load task. However, when the attentional load of the task used to divert attention from the faces was increased (i.e., in the identity task), the differential amygdala response to emotional versus neutral unattended faces vanished; consistent with the proposal that amygdala processing depends on the attentional resources available.

A similar conclusion has been put forward for faces presented at fixation, while attention was oriented towards the periphery for a bar-orientation matching task (Pessoa et al., 2002, 2005) or when participants were performing a letter search task superimposed on a face (Bishop et al., 2007; Mitchell et al., 2007), but the evidence for peripheral faces had remained inconclusive. Previous data have rather suggested that attentional-load manipulations might not influence discriminative responses of the amygdala to peripheral neutral and emotional faces, or at least do so to a lesser extent than for foveal stimuli (Vuilleumier et al., 2001; Williams et al., 2005). However, this suggestion was mainly based on indirect evidence, stemming from the comparison of separate experiments thought to involve different attentional-load manipulations, but using different designs and different participants. The present study reaches a different conclusion based on less equivocal comparisons. First, attentional load was manipulated within participants, which can be of paramount importance since individual differences might play a non-negligible role in the effects studied here. For example, Bishop and collaborators (2004, 2007) showed that the emotion–attention interaction in the left (but not the right) amygdala can be modulated by anxiety. Second, attentional load was manipulated by changing the kind of matching task the participants had to perform, but the stimulus displays were exactly the same in both tasks. Third, the efficacy of the attentional manipulation was substantiated by behavioural as well as by fMRI data. Importantly, our behavioural data included a direct measure of the residual processing of the task-irrelevant face stimuli (recognition task). Our results therefore suggest that, just as the processing of foveal facial expressions (Bishop et al., 2007; Mitchell et al., 2007; Pessoa et al., 2002,

2005), the processing of extra-foveal facial expressions in the amygdala can be gated by spatial attention when difficult perceptual discriminations are required. In other words, attentional resources appear to play a role in the processing of emotionally relevant information, even when this information is provided outside of foveal vision, and the amount of processing allowed seems to depend on the extent to which the task used to divert attention does or does not exhaust processing resources.

As mentioned earlier, ignoring neutral stimuli at fixation or in the periphery may involve different mechanisms (Beck and Lavie, 2005), and irrelevant peripheral faces may have a special status with regard to the perceptual load theory (Lavie et al., 2003). Results from experiments using event-related potentials (ERPs) also indicate that the emotional processing of unattended faces may differ when they are presented at fixation or in the periphery. For peripheral unattended faces, emotion-specific ERP modulations are completely eliminated (Eimer et al., 2003; Holmes et al., 2003), but for foveal unattended faces, the earlier part of these modulations (before 220 ms) are preserved (Holmes et al., 2006). These results could reveal the existence of differences in the ability of foveal and extra-foveal stimuli to trigger early and late, more controlled, stages of emotional processing under condition of inattention. However, these studies may not only differ on the spatial locus of presentation of the face stimuli, but also on the attentional load of the tasks used to divert attention from the faces. To our knowledge, the effects of attentional load on the emotional processing of peripheral faces have not yet been investigated with ERPs (but see Doallo et al., 2006 for a study using affective pictures). Moreover, ERPs can reflect subtle and transient effects that may not be evident from fMRI results, and it is unlikely that the emotional effects observed in ERP experiments directly reflect amygdala activation (given its electrically closed structure and its deep position). Thus, whether the similar effects of attentional load observed for central and peripheral unattended faces in the amygdala relies on the same attentional control/cognitive mechanisms remains an important issue to investigate in the future.

In the current experiment, the attentional-load manipulation was verified to be highly effective in both the behavioural and fMRI experiments. Participants were consistently faster and committed fewer errors in the orientation task than in the identity task. The face-recognition test introduced in the behavioural experiment showed that the fearful expression of unattended faces (but not their identity) could be discriminated above chance in the orientation task only. Therefore, the behavioural results of the present study suggest that

the identity task was more attention-consuming than the orientation task, and that some coarse emotional information could be extracted from task-irrelevant stimuli only in the low-attentional-load task.

Our attentional manipulation was also validated by the occurrence of different patterns of activation in several cortical regions. Consistent with previous studies (e.g., Anderson et al., 2003; Vuilleumier et al., 2001; Williams et al., 2005; Wojciulik et al., 1998), we found that the right fusiform gyrus (FG) was more activated when attention was oriented to faces rather than houses, whereas the activation in the right parahippocampal gyrus (PHG) was greater when attention was oriented to houses rather than faces. We also found that this effect was modulated by the task performed by the participants. Indeed, in both areas, the difference of activation produced by the preferred stimulus for this area at relevant versus irrelevant locations was bigger in the identity than in the orientation task. Similar results were obtained in the right STS. Evidence regarding the modulation of this area as a function of selective attention remained relatively sparse (Vuilleumier et al., 2004; Williams et al., 2005). Altogether, these fMRI data complement the behavioural data, and provide further evidence that the tasks used differed in terms of attentional load.

At this point, we would like to underline that we did not observe a complete suppression of amygdala activation for unattended fearful and neutral faces in the high-load task (comparison against baseline: both $p<.05$, one-tailed), consistent with the results reported by Pessoa et al. (2005) (see also Taylor and Fragopanagos, 2005, for simulation data). Pessoa et al. (2005) suggested that complete suppression of amygdala responses to unattended faces may occur only when there are scarcely no attentional resources available for their processing. Up to this point, intermediate levels of inattention would render the emotional expression of unattended faces increasingly ambiguous, which could lead to undifferentiated amygdala activation (Whalen, 1998). In other words, when attention is more and more efficiently diverted from the faces (up to a certain level), amygdala responses could gradually lose their specificity. Consistent with this view, previous studies have found, that when unattended fearful faces led to more amygdala activation than unattended neutral faces, a significant increase in amygdala activity could be observed for unattended versus attended expressions of disgust (Anderson et al., 2003) or happiness (Williams et al., 2004). These data suggest that, while there is something specific about amygdala responses to fearful faces under conditions of focused attention, amygdala processing could be more broadly tuned to other facial expressions under conditions of reduced attention, responding more strongly and non-selectively to any emotion-laden information (probably with a bias in favour of threatening information, Williams et al., 2005; see Palermo and Rhodes, 2007). This is consistent with the proposal that emotional processing in the amygdala mostly relies on coarse visual information conveyed by the magnocellular visual pathway (Vuilleumier et al., 2003; Winston et al., 2003). Our data might imply that, when inattention only allows an even coarser processing of facial features, the presence of face stimuli would still be registered by the amygdala (probably due to their general relevance, see Posamentier and Abdi, 2003; Palermo and Rhodes, 2007), whereas the differential responses to neutral and emotional faces would be suppressed. This is consistent with the fact that we observed quite a strong fusiform activation for unattended faces even in the identity task, and could explain why the processing of faces in general tend to be prioritized regardless of their task relevance (see Lavie et al., 2003, and Palermo and Rhodes, 2007, for a review).

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