

# Neural processing of emotional faces requires attention

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Contributed by L. G. Ungerleider, July 8, 2002

**Attention gates the processing of stimuli relatively early in visual cortex. Yet, existing data suggest that emotional stimuli activate brain regions automatically, largely immune from attentional control. To resolve this puzzle, we used functional magnetic resonance imaging to first measure activation in regions that responded differentially to faces with emotional expressions (fearful and happy) compared with neutral faces. We then measured the modulation of these responses by attention, using a competing task with a high attentional load. Contrary to the prevailing view, all brain regions responding differentially to emotional faces, including the amygdala, did so only when sufficient attentional resources were available to process the faces. Thus, the processing of facial expression appears to be under top-down control.**

To what extent are unattended objects processed by the visual system? Psychophysical evidence suggests that processing outside the focus of attention is attenuated and may even be eliminated under some conditions (1–4). For example, “change blindness” studies show that subjects may fail to report even very large changes in complex scenes (2). Even low-level tasks commonly thought to be “preattentive,” such as orientation pop-out, may require attention to be successfully performed (3). Likewise, at the neural level, functional MRI responses in the middle temporal area to moving stimuli are essentially eliminated when subjects are engaged in a competing task with high attentional load (4). Taken together, these studies suggest that perception and its underlying neural substrate may be abolished if attentional resources are completely consumed by a competing task.

A major exception to this critical role of attention may be the neural processing of emotional stimuli, which are reported to be processed automatically, namely, without attention (5, 6). Subjects exhibit fast, involuntary autonomic responses to emotional stimuli, such as aversive pictures or faces with fearful expressions (7, 8). Other behavioral studies suggest that the visual processing of facial expression occurs not only automatically but may even take place without conscious awareness (5). This conclusion is also supported by imaging studies of the amygdala, a structure important for the processing of fear (9, 10). Such studies report that the amygdala is activated not only when normal subjects view fearful faces, but even when these stimuli are masked and subjects appear to be unaware of them (11, 12). The view has thus emerged that the amygdala is specialized for the fast detection of emotionally relevant stimuli in the environment, and that this can occur without attention and even without conscious awareness.

In the present study, we tested the alternative possibility, namely, that the neural processing of emotional stimuli is not automatic and requires some degree of attention, similar to the processing of other stimulus categories. We hypothesized that the failure to modulate the processing of emotional stimuli by attention in previous studies was caused by a failure to fully engage attention by a competing task. We therefore used functional MRI and measured activations in the amygdala and other brain regions that responded differentially to faces with emotional expressions (fearful and happy) compared with neutral faces and then examined how these responses were modu-

lated by attention. In designing our competing task, we chose one that was sufficiently demanding to exhaust attentional resources on that task and leave little or none available to process faces.

## Materials and Methods

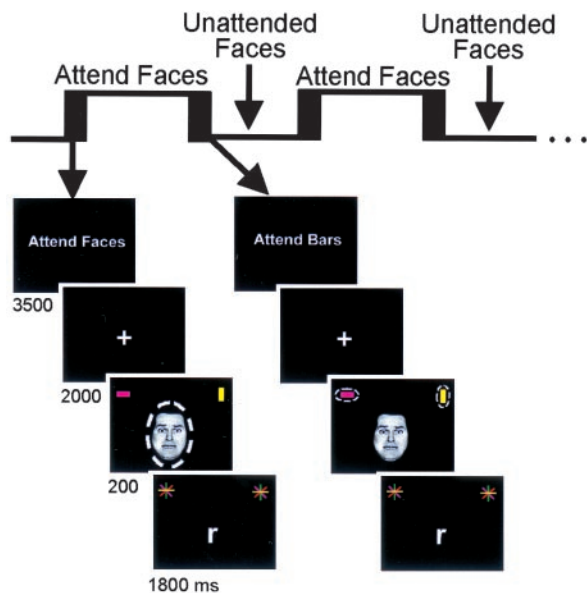
**Subjects.** Twenty-one healthy subjects (eight women, 22–38 years old) participated in the study, which was approved by the National Institute of Mental Health Institutional Review Board. All subjects were in good health with no past history of psychiatric or neurological disease and gave informed written consent.

**MRI Data Acquisition.** Images were acquired with a 1.5-Tesla General Electric Signa scanner. Functional images were taken with a gradient echo echo-planar imaging sequence (repetition time = 3.5 s; echo time = 40 ms; field of view = 24 cm; flip angle = 90°; 64 × 64 matrix). Whole-brain coverage was obtained with 36 sagittal slices (thickness, 4 mm; in-plane resolution, 3.75 × 3.75 mm). Echo-planar images were coregistered to a high-resolution anatomical scan of the same subject’s brain taken in the same session (three-dimensional Spoiled GRASS; repetition time = 15 ms; echo time = 5.4 ms; field of view = 24 cm; flip angle = 45°; 124 sagittal slices; thickness = 1.2 mm; 256 × 256 matrix).

**Task.** A fearful, happy, or neutral face (2°) was presented at fixation with bars (0.2° each) in the left and right periphery (5.7° eccentricity) for 200 ms, which precluded deliberate saccades during their presentation. Faces were taken from Ekman’s series. The bars were then masked and an r appeared at fixation for 1,800 ms, prompting subjects to respond with left or right button presses. Each trial was followed by a 3,500-ms blank screen (Fig. 1). In attended trials, subjects indicated whether the face was male or female. In unattended trials, subjects indicated whether the bars were of similar orientations (i.e., both close to horizontal or both close to vertical) or of dissimilar orientations. Visual stimuli were identical for both conditions, the subjects always fixated the faces, and only the focus of attention alternated between faces and bars. Each block of trials was cued by an instruction display and contained four trials in which face type and bar orientations were randomly chosen. Thus, ours was a hybrid design with a general block structure (attended/unattended), and an event-related structure (facial expression) within each block, i.e., essentially a factorial design with an attentional factor (two levels) and a valence factor (three levels). Subjects were scanned for a total of four to five runs, each consisting of eight attended and eight unattended blocks. During a practice session, eye movements were inspected and subjects were given feedback until they reliably maintained fixation. Note that if subjects did not consistently maintain fixation on the faces, then on unattended trials the face stimuli would have activated a more peripheral part of the visual field representation in early retinotopically organized areas, a finding we did not observe.

Abbreviations: ROI, region of interest; STS, superior temporal sulcus; VMPFC, ventromedial prefrontal cortex; OFC, orbitofrontal cortex.

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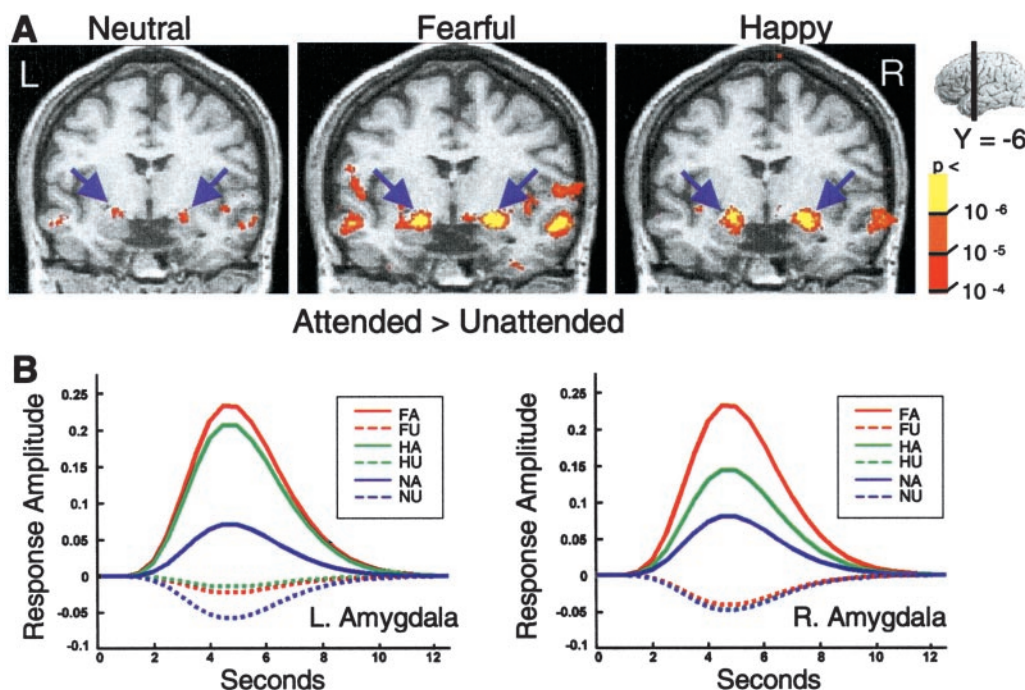
**Fig. 1.** Experimental paradigm. While subjects fixated the faces, they indicated in alternating blocks of trials either whether the face was male or female (attended trials) or whether the bars were or were not of similar orientations (unattended trials). The dashed lines indicate the display regions attended on alternating blocks (not shown on actual displays). Stimuli are not drawn to scale.

**Eye Movement Acquisition.** Infrared video-oculography (RK-726PCI Pupil Tracking System, ISCAN, Burlington, MA) was used to continually sample eye position at 60 Hz in a separate experimental session. To assess deviations from fixation for the two tasks and face type, horizontal and vertical eye position were

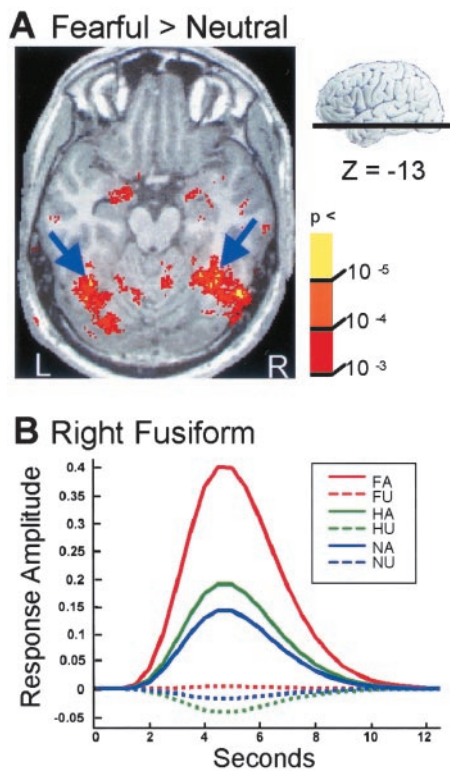
determined for a 200-ms window after the fixation stimulus and for the 200-ms window comprising the stimulus display.

**Data Analysis.** Our data analysis proceeded in two steps. In a first-level analysis, we used a general linear model (13) as implemented in AFNI (14). This process represents a voxel-based approach allowing the construction of statistical maps that reflect the significance of evoked responses, in relation to the precision with which these responses could be measured (i.e., within-subject error variance). Because our inferences were made on the basis of a second-level analysis (see below) we report these results without correction for multiple comparisons. This procedure enabled us to summarize the response profiles in a comprehensive fashion. In a second-level analysis, we used the parameter estimates (beta weights) pertaining to specific event-related responses as a dependent measure in a conventional repeated-measures ANOVA. This procedure corresponds to a random-effects analysis in which our inferences are in relation to inter-subject variability. To eschew the multiple comparisons procedure we restricted our analyses to a small number of predefined regions of interest (ROIs), defined on the basis of independent (localizer) data. A standard *P* value of 0.05 was used as the criterion for statistical significance. Data were smoothed with an isotropic 8-mm Gaussian kernel (full width at half maximum). Averaged-across-subjects parameter estimates were used to illustrate the effects of valence and attention for each ROI (Figs. 2 and 3). The general linear model used in the first level contained regressors based on “stick functions” convolved with a hemodynamic response function (15) to model the event-related responses for each of the six trial types.

ROIs were determined by a combination of anatomical and functional information. Initially, masks for the amygdala, fusiform gyrus, superior temporal sulcus (STS), and ventromedial prefrontal cortex/orbitofrontal cortex (VMPFC/OFC) were defined on anatomical grounds for each individual. Within these



**Fig. 2.** Attention and valence effects in the amygdala. (A) Arrows point to the amygdala. Attended faces compared with unattended faces evoked significantly greater activations for all facial expressions. The level of the coronal section is indicated on the small whole-brain inset. L, left; R, right. (B) Estimated responses for the left and right amygdala ROIs as a function of attention and valence. FA, fearful attended; FU, fearful unattended; HA, happy attended; HU, happy unattended; NA, neutral attended; NU, neutral unattended. Coordinates (*x*, *y*, *z*) for peak sites in the amygdala were: neutral, left,  $-20, -8, -9$ , right,  $21, -4, -10$ ; fearful, left,  $-18, -6, -10$ , right,  $20, -5, -9$ ; happy, left,  $-18, -5, -9$ , right,  $21, -5, -9$ .



**Fig. 3.** Attention and valence effects in ventral occipitotemporal cortex. (A) Fearful faces compared with neutral faces (pooled across attentional conditions) evoked significantly greater activations. Arrows point to the fusiform gyrus. L, left; R, right. (B) Estimated responses for the right fusiform gyrus ROI as a function of attention and valence.

masks, we averaged the time series of voxels that were responsive to face stimuli for each individual, according to two to three separate “face localizer” runs. Each run included blocks containing neutral faces, nonface objects, and phase-scrambled control stimuli. A face-responsive region was one in which faces elicited greater responses than scrambled control stimuli (for the amygdala,  $P < 0.05$ ; for all other regions,  $P < 0.01$ ; both uncorrected). Thus our ROIs were defined independent of the main experimental runs. Mean Talairach coordinates for our masks were as follows: fusiform gyrus, left,  $x = -37$ ,  $y = -47$ ,  $z = -14$ , right,  $x = 39$ ,  $y = -46$ ,  $z = -15$ ; STS, left,  $x = -47$ ,  $y = -62$ ,  $z = 18$ , right,  $x = 50$ ,  $y = -62$ ,  $z = 17$ ; VMPFC/OFC,  $x = 5$ ,  $y = 48$ ,  $z = -4$ ; see Fig. 2 for amygdala coordinates.

The ROI random-effects analysis was complemented by a whole-brain voxel-wise, fixed-effects analysis. Statistical group maps were obtained by combining individuals’ maps into a composite final Z-map. Each individual’s brain was transformed with AFNI into Talairach space and then combined (averaged together and multiplied by the square root of the number of subjects). Because this latter analysis is uncorrected for multiple comparisons, more stringent  $P$  values were chosen (at least  $P < 0.001$ ) for statistical significance.

To assess increases in coupling between the amygdala and other brain regions, a psychophysiological interaction analysis was used (16). The key term of this analysis is an interaction term involving brain activity (i.e., the peak voxel in the amygdala for the contrast between attended and unattended trials) and a psychological variable (i.e., the difference of the regressors modeling attended and unattended trials). Note that both the physiological and psychological variables were entered into the multiple regression model; in this way, the results cannot be

explained by the main effects of either, but only by the interaction or increase in coupling.

## Results

**Behavioral Results.** Median reaction times and accuracy in the face gender and bar orientation tasks were determined for 15 of the 21 subjects; because of equipment malfunction, behavioral data from six subjects were not analyzed. Overall performance on the face gender task was 91% correct and reaction time was 661 ms. Overall performance on the bar orientation task was 64% correct and reaction time was 1,005 ms, indicating that it was, as intended, a very demanding task. Planned comparisons revealed that there was no difference in reaction time for the bar orientation task as a function of the type of unattended face stimulus (mean  $\pm$  SD: neutral,  $995 \pm 226$  ms; fearful,  $1,015 \pm 233$  ms; happy,  $1,006 \pm 245$  ms;  $P > 0.05$ , repeated-measures ANOVA).

**Eye-Tracking Results.** A separate group of 11 subjects participated in an eye-tracking session in which the same task and stimuli used in the functional MRI session were used. The mean vertical displacement from fixation was  $0.75^\circ$  for the bar orientation task and  $0.70^\circ$  for the face gender task; the mean horizontal displacement from fixation was  $1.22^\circ$  for the bar orientation task and  $1.12^\circ$  for the face gender task. A repeated-measures ANOVA showed no differential horizontal and vertical eye movements as a function of task, valence of the faces, or the interaction between the two main effects ( $P > 0.05$ ). Moreover, behavioral performance on the eye-tracking session did not differ significantly from that obtained during the functional MRI session ( $P > 0.05$  for both reaction times and % correct), indicating that for the bar orientation task, covert shifts of attention were sufficient to allow subjects to attain the level of performance observed in the scanner.

**Face Responsive Regions.** We first determined the network of brain regions responsive to face stimuli by using localizer runs in which subjects viewed neutral face, (nonface) object, and scrambled-face stimuli. The main sites activated by the comparison of face vs. scrambled-face stimuli ( $P < 0.00001$ , uncorrected) included occipitotemporal visual regions (including the fusiform gyrus) and the STS, as reported in the past (17, 18). This contrast also revealed activation of the amygdala and VMPFC/OFC; the latter included sites in the rectus gyrus and the immediately adjacent supraorbital sulcus above it. Subsets of voxels within all these regions were also strongly activated by the comparison of face vs. nonface object stimuli, showing that the responses within these regions were selective for faces and not unspecific effects of visual stimulation. Next, we investigated whether activations in the regions within this “face network” were affected by stimulus valence and attention.

**Amygdala.** As shown in previous studies (6, 11, 12, 19, 20), fearful faces produced greater activation than neutral faces in the amygdala, as revealed by the analysis of attended trials only; this effect was bilateral (left,  $x = -18$ ,  $y = -6$ ,  $z = -12$ ; right,  $x = 23$ ,  $y = -7$ ,  $z = -12$ ). Attended compared with unattended faces evoked significantly greater activations bilaterally for all facial expressions (Fig. 2A). Although our activations were a little superior to those found in some studies (20), they were very close to the dorsal amygdala findings reported by other investigators (11, 19). Using a  $P = 0.05$  ( $P = 0.01$ ) uncorrected threshold, a greater response to attended compared with unattended faces was observed for fearful faces in 14/21 (10/21) individual subjects, for happy faces in 16/21 (12/21) subjects, and for neutral faces in 9/21 (7/21) subjects.

To further characterize the effects of valence and attention, we performed a random-effects analysis on the amygdala ROI,

**Table 1. Regions in which there was a significant valence by attention interaction: The valence effect was greater for attended compared to unattended conditions**

Area	Contrast								Brodmann Area
	Fearful (F) > Neutral (N)				Fearful (F) > Happy (H)				
	L/R	Talairach coordinates			L/R	Talairach coordinates			
	X	Y	Z	X	Y	Z			
Calcarine		0	-75	7		1	-74	5	17/18
MOG/IOG					L	-34	-83	-7	18/19
					R	33	-83	-7	18/19
MOG					L	-43	-73	10	19/39
					R	45	-66	13	19/39
Fusiform gyrus	L	-38	-49	-19	L				37
	R	21	-57	-12	R	17	-53	-12	19
STS (anterior)	L	-52	-21	1	L	-58	-38	11	22
STS (posterior)	R	45	-45	22	R	45	-58	18	22 (F > N); 37 (F > H)
Amygdala	L*	-19	-6	-10	L	-20	-9	-19	
	R	25	-7	-9	R				
Accumbens	L*	-9	-9	-8					
	R*	11	9	-9					
Insula	L	-51	-6	9					6/22
	R	45	-5	4					6/22
Ant. cingulate					R	9	33	4	24
VMPFC/OFC					R	10	47	-13	11
Medial FP		0	53	8					10

For all regions,  $P < 0.001$  (uncorrected) for valence by attention interaction, except those regions indicated with an asterisk (\*) where  $P < 0.005$ . Ant: anterior; FP: frontal pole; IOG: inferior occipital gyrus; MOG: middle occipital gyrus; L, left; R, right.

which revealed that the main effect of attention was significant on both the left and right ( $P < 0.005$ ). There was also a significant effect of valence for the left amygdala ( $P < 0.05$ ), such that both fearful and happy faces evoked greater activations than neutral faces. For the right amygdala, there was a significant difference only between fearful and neutral faces ( $P < 0.05$ ). Importantly, for the left amygdala, there was a significant interaction between stimulus valence and attention ( $P < 0.05$ ), that is, the differential response to stimulus valence was observed only in the attended condition (Fig. 2B); for the right amygdala we observed a trend ( $P = 0.11$ ). For the unattended condition, responses to all stimulus types were equivalent (i.e., not statistically different,  $P > 0.05$ ; Fig. 2B) and not significantly different from zero ( $P > 0.05$ ). Thus, amygdala responses to emotional stimuli are not automatic and instead require attention.

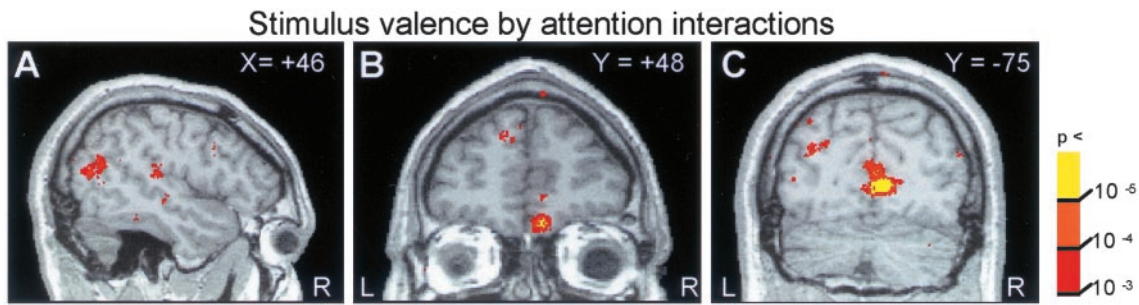
**Occipitotemporal Visual Cortex.** Consistent with prior reports (6, 17, 21), activations to faces in this ventral cortical region were modulated by attention; the strongest sites were observed in the fusiform gyrus (Brodmann Area 20/37; left,  $x = -32, y = -37, z = -15$ ; right,  $x = 35, y = -41, z = -15$ ), the posterior middle occipital gyrus (Brodmann Area 18; left,  $x = -32, y = -85, z = -11$ ; right,  $x = 31, y = -87, z = -5$ ), and the lingual gyrus (Brodmann Area 18; left,  $x = -16, y = -93, z = -8$ , right,  $x = 24, y = -91, z = -6$ ). Like activations in the amygdala, those throughout ventral occipitotemporal cortex were also modulated by stimulus valence, in that fearful faces evoked greater activation than either happy or neutral ones (Fig. 3A and B).

We further characterized the effects of stimulus valence and attention in ventral occipitotemporal cortex by performing an ROI analysis on the fusiform gyrus. The main effects of valence and attention were significant bilaterally ( $P < 0.005$ ). There was also a significant valence by attention interaction bilaterally (left,  $P < 0.05$ ; right,  $P < 0.01$ ), such that the enhanced activations evoked by fearful faces occurred only in the attended condition (Fig. 3B). Again, activations evoked by unattended faces were not significantly different from zero ( $P > 0.05$ ).

**Other Brain Regions.** To determine how the effects of valence depended on attention, we searched for voxels throughout the brain with a significant interaction between the two main effects, namely, voxels in which the valence effect differed for attended and unattended conditions. Differential effects of valence as a function of attention were observed not only in the amygdala and occipitotemporal areas, but also in other brain regions (Table 1). A significant interaction between valence and attention was found in the calcarine fissure, right posterior, and left anterior STS for the contrast of both fearful compared with neutral and fearful compared with happy faces (Fig. 4). This interaction was found in bilateral insula, bilateral nucleus accumbens, and medial frontal pole for the contrast of fearful compared with neutral faces only, indicating that these regions responded to attended, happy faces. Finally, this interaction was found in the right anterior cingulate gyrus and the right VMPFC/OFC (Fig. 4) for the contrast of fearful compared with happy faces.

To further characterize the effects of stimulus valence and attention, we performed an ROI analysis on the STS and VMPFC/OFC. For the left STS there was a main effect of attention ( $P < 0.01$ ) and a significant valence by attention interaction ( $P < 0.01$ ), but no significant effect of valence ( $P > 0.05$ ). For the right STS there was a main effect of attention ( $P < 0.05$ ); the main effect of valence and the valence by attention interaction approached significance ( $P = 0.052$  and  $P = 0.056$ , respectively). For the VMPFC/OFC, there was a significant main effect of attention ( $P < 0.005$ ) and a significant valence by attention interaction ( $P < 0.005$ ). In all of the above ROIs, the significant interaction arose from fearful faces eliciting stronger responses than happy or neutral faces ( $P < 0.05$ ), but only when faces were attended.

Finally, we also probed the calcarine fissure at the ROI level. Because this region was not evident in the contrast of faces vs. scrambled stimuli, for this ROI we pooled voxels that responded to any task component. Both the main effect of valence ( $P < 0.05$ ) and the valence by attention interaction ( $P < 0.01$ ) were significant, but the main effect of attention was not ( $P > 0.05$ ).



**Fig. 4.** Stimulus valence by attention interaction effects. Maps indicate voxels in which the valence effect was greater for attended compared with unattended conditions. (A) STS: interaction between valence and attention for fearful compared with happy faces. (B) VMPFC/OFC: interaction between valence and attention for fearful compared with happy faces. (C) Calcarine fissure (V1/V2): interaction between valence and attention for fearful compared with neutral faces. L, left; R, right.

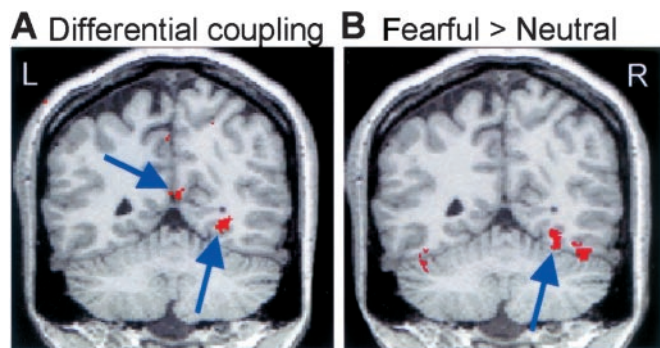
**Differential Coupling.** In our study, in the presence of attention, activations in several regions outside the amygdala were modulated by valence. This finding suggests that the amygdala may have been the source of this modulation (20, 22), which is consistent with its widespread projections to cortical sensory processing areas (23). We explored this issue by examining the coupling between left amygdala activity and activity in other brain regions (so-called psychophysiological interaction analysis; ref. 16). To do so, we tested for condition-dependent changes in functional connectivity, an analysis that highlights changes in the coupling between brain regions. The results revealed that ventral occipitotemporal cortex, including the middle occipital and the fusiform gyri, exhibited increased coupling with the amygdala during attended compared with unattended trials, a finding consistent with a modulatory role for the amygdala. Fig. 5 illustrates the site of the fusiform-enhanced coupling and, for comparison, at the same slice level, the contrast of fearful and neutral faces during attended trials, as this modulation is hypothesized to originate in the amygdala. Note the striking similarity between the two maps. Interestingly, we also found increased coupling between the amygdala with the calcarine fissure on attended trials, which is consistent with projections to very early visual areas, including V1 and V2, from the amygdala (23). Increased coupling with the amygdala was not restricted to occipitotemporal regions, but also included the STS, VMPFC, and OFC, as well as parietal and other frontal regions. Although the data are therefore consistent with a modulatory role for the

amygdala, this kind of analysis cannot be definitive on the issue of directionality.

### Discussion

In the present study, we addressed the question of whether the processing of emotional stimuli occurs automatically, or whether it requires some degree of attention. Contrary to the prevailing view, we found that all brain regions responding differentially to faces with emotional content, including the amygdala, did so only when sufficient attentional resources were available to process those faces. Indeed, when all attentional resources were consumed by another task, differential responses to emotional expression were eliminated. Thus, it does not appear that faces with emotional expressions are a “privileged” category of objects immune to the effects of attention. Consistent with Lavie’s proposal (1), we propose that the bar task exhausted processing capacity and that stimuli irrelevant to that task (i.e., faces) were not processed. Strong evidence for this notion comes from the fact that the parameter estimates associated with unattended faces were not significantly different from zero. This was the case even though each trial started with a 2-s fixation and ended with a 3-s blank period (i.e., slow-rate event related), which presumably would have produced signal increases had resources been available to process the unattended stimuli.

The present findings are in direct contrast to those of Vuilleumier *et al.* (6) who also studied the effects of attention and valence on face processing, using a variation of the task used by Wojciulik *et al.* (21). Subjects fixated a central cue and matched either two faces or two houses presented eccentrically. In their study, as in ours, fearful faces compared with neutral ones evoked greater activation in the fusiform gyrus, which was modulated by attention. However, unlike our results, they failed to see evidence that attention modulated responses in the amygdala, regardless of stimulus valence. The most likely explanation for their negative results is that the attentional manipulation in the Vuilleumier *et al.* study was not as effective as in the present study. First, behavioral performance for the bar orientation task in the present study and house matching in their study was 64% and 86% correct, respectively, indicating that our competing task was a more demanding one. Second, they found fusiform responses for both fearful and neutral faces even in the absence of attention; a similar finding was obtained by Wojciulik *et al.* In our study, by contrast, no significant fusiform responses to unattended faces were observed (Fig. 3B), again indicating that our competing task was more demanding. Third, in the Vuilleumier *et al.* study, reaction times while subjects matched the houses were slower when unattended faces were fearful than when they were neutral, suggesting that they captured attentional resources away from the processing of the houses. In our study, by contrast, no difference in reaction time during the bar



**Fig. 5.** Coupling of activity between the amygdala and other brain regions. (A) Increases in the coupling between amygdala and visual cortical activity (V1/V2 and fusiform gyrus; see arrows) on attended compared with unattended trials (see *Materials and Methods*). (B) Contrast of fearful and neutral faces during attended trials, demonstrating a significant effect of valence in the fusiform gyrus. A threshold of  $P < 0.00001$  (uncorrected) was used for both A and B (which show the  $y = -52$  plane). L, left; R, right.

orientation task was observed as a function of the emotional content of the unattended face, indicating that fearful faces did not capture attentional resources. Finally, the failure to show a significant attention by valence interaction does not constitute evidence that there is no interaction, as this would be accepting the null hypothesis. Thus, the difference between the two studies likely reflects the extent to which the competing tasks did or did not exhaust processing resources.

The involvement of the amygdala in the processing of fear has been repeatedly demonstrated (9, 10). However, its involvement in nonthreat-related functions is an open question (24, 25). In the present study, we also observed differential responses evoked by happy compared with neutral faces in the left amygdala, a finding reported in a previous investigation (26) and consistent with a role for the amygdala that encompasses affective processing beyond the detection of threat (10). In fact, we also observed amygdala activation for neutral faces when compared with both scrambled-face stimuli and nonface objects (in localizer runs).

Our data reveal that the effects of valence depended on attention not only in the amygdala, but also in several additional brain regions, including the fusiform gyrus, STS, VMPFC/OFC, and the calcarine fissure (V1/V2). It is likely that such valence-dependent responses result from feedback from the amygdala, which has been proposed to modulate sensory processing according to stimulus valence (20, 22), an idea consistent with both known anatomical projections from the amygdala to all of the aforementioned structures, including V1 (23), and the results of our functional connectivity analysis. We propose that the amygdala is a key source of the valence effect, which is then transmitted to other brain regions.

If the amygdala conveys valence to sensory stimuli, what is the pathway by which it receives its sensory inputs? Our results do not favor the idea of an automatic subcortical route, as has been proposed by others (27). First, whereas responses to faces were observed in cortex, they were not found in any subcortical structures other than the amygdala, a finding consistent with single-cell studies. Second, a truly automatic pathway should not depend on attentional resources, yet differential amygdala responses to valence were eliminated when these resources were

depleted. We therefore suggest that the critical pathway for the processing of emotional expressions is not subcortical but rather proceeds from V1 to extrastriate areas, including fusiform and STS, and then to the amygdala. Thus, unlike simple acoustic stimuli that are typically used in fear conditioning, for which subcortical processing may be sufficient (28), for detailed form information required for face perception, a cortical pathway might be necessary.

Although our results indicate that attentional resources are required for differential responses to valence, they do not imply that humans are unable to respond to potential threats outside the focus of attention or that the amygdala only responds to attended stimuli. It has been shown that negative stimuli, compared with positive ones, are a more effective source of involuntary interference to ongoing tasks (29) and more readily recruit attention (30). Moreover, under certain circumstances, amygdala responses are evoked by unattended faces (6) as well as by masked faces of which subjects are presumably unaware (11, 12). In all of these instances, however, it is possible that attentional resources to the unattended or masked emotional stimuli were not sufficiently reduced by a competing task. For example, in the case of masked faces, subjects were required to direct attention to the location of the stimuli in the absence of any competing task, suggesting that attentional resources were available to allow subliminal responses to emotional stimuli. Thus, while attention appears to be necessary for the processing of faces with emotional expressions, it may not ensure that they reach awareness.

We thank David Perrett for providing us with face stimuli, Elizabeth Hoffman for providing us with stimuli for the face localizer runs, Rene Hill for assistance with scanning, Djalma Pessoa for statistical advice, Adam Greenberg and John Ingeholm for assistance with eye tracking, and Robert Desimone, Jim Haxby, and Alex Martin for invaluable suggestions on an earlier version of the manuscript. This study, supported by the National Institute of Mental Health-Intramural Research Program, was conducted while M.M. was a Howard Hughes Scholar at the National Institutes of Health.

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