Crossmodal binding of fear in voice and face

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In social environments, multiple sensory channels are simultaneously engaged in the service of communication. In this experiment, we were concerned with defining the neuronal mechanisms for a perceptual bias in processing simultaneously presented emotional voices and faces. Specifically, we were interested in how bimodal presentation of a fearful voice facilitates recognition of fearful facial expression. By using event-related functional MRI, that crossed sensory modality (visual or auditory) with emotional expression (fearful or happy), we show that perceptual facilitation during face fear processing is expressed through modulation of neuronal responses in the amygdala and the fusiform cortex. These data suggest that the amygdala is important for emotional crossmodal sensory convergence with the associated perceptual bias during fear processing, being mediated by task-related modulation of face-processing regions of fusiform cortex.

An organizational principle within the central nervous system is that inputs from diverse sensory systems converge in a variety of brain regions (1). Sensory convergence facilitates linkage of external events to a common causal reference frame in the service of adaptive responses. Consequently, inputs from one sensory modality can influence perceptual sensitivity in another modality (2). Psychological data indicate that bimodal or multimodal inputs are likewise important in emotional perception. Thus, when subjects view emotional faces in combination with emotional voices, information from both modalities is combined in making affective judgements as, for example, when a fearful face is more likely to be perceived as fearful if accompanied by a fearful voice (3).

Recent evidence for crossmodal emotional perceptual effects is provided by experiments where pairing an emotional face with a congruent emotional voice leads to a facilitation in facial emotional recognition (4). These behavioral findings indicate an expression-specific voice-biasing effect with no effect of neutral voice. Crossmodal effects in perception of emotion are also evident in infants who dwell longer on a face when accompanied by an emotionally congruent, as opposed to an incongruent, voice (5). Behavioral and neurophysiological studies show that crossmodal emotional influences are expressed bidirectionally across sensory modalities (1, 6, 7). This effect is mandatory and preattentive in so far as it is observed even during bimodal auditory-visual tasks in which subjects receive instructions to either ignore the voice or face but are also given a visual or auditory attention-demanding secondary task (8).

In this report, we address how crossmodal biasing effects from emotional voices on the perception of emotional faces are expressed at the level of brain function. Specifically, we were interested in crossmodal integration during fear processing in that we could advance a specific hypothesis for involvement of the amygdala (9). Furthermore, in the light of previous data indicating fear-specific influences of amygdala activation on fusiform cortex response during processing of fearful faces (10), we predicted that crossmodal fear-congruency effects, in a face-processing task, would be expressed by an associated modulation of face-processing regions of the fusiform cortex.

Our experimental paradigm combined event-related functional MRI (efMRI) with bimodal presentation of faces (on a screen) and voices (via headphones). During each trial, a still photograph appeared depicting either a facial expression of fear (F) or of happiness (H) while, simultaneously, subjects heard a voice uttering a short sentence in either a happy (h) or a fearful tone (f) (see Fig. 1*a* for details). The faces were intermediate in intensity between neutral and canonical expressions of fear or happiness. These intermediate levels of emotional expression were chosen on the basis of previous behavioral data indicating that they corresponded to levels of expression that are maximally susceptible to crossmodal effects (11). Thus, in this experimental design the two levels of facial expression (F and H) were crossed with the two levels of vocal expression (f and h).

Methods

Subjects. Twelve native Dutch-speaking subjects (4 male, 8 female, mean age 25 years) participated in the study. Nine were right-handed and three were left-handed. Subjects had no history of neurological or psychiatric problems and were not taking any medication at the time of the study. All subjects gave informed consent, and the study was approved by the Joint Ethics Committee of the National Hospital and Institute of Neurology, London.

Stimuli. The faces were of two emotional classes, fearful and happy, depicting 50% of either emotion realized through the following manipulation. Prototypical examples of neutral, fearful, and happy faces were obtained from the Ekman series. By using computer-morphing procedures, incremental shifts of 25% between the neutral and emotional pictures were created. From this new set, exemplars of either 50% fearful or happy faces were obtained and used as our target stimuli. Presentation of these target emotional faces was crossed with presentation of auditory stimuli involving brief sentences spoken in either a fearful or happy tone (see Fig. 1*a*). The duration of these sentences, spoken in Dutch, averaged 2 sec. An identical content was used in both sentence types, happy and fearful, with only the emotional prosody being varied. The specific sentence provided was "His girlfriend came by plane." The stimulus onset asynchrony (SOA) between voice and face was fixed at 650 msec.

Auditory materials were prepared as follows. Six male actors were instructed by means of examples of real-life situations to pronounce neutral sentences ("His girlfriend came by plane") with different emotional tones of voice (angry, afraid, happy, sad, disgusted, or neutral). For each actor, and each tone of voice, three different speech samples were recorded on a DAT recorder, digitized, and amplified (using SOUNDEDIT 16 1.0 b4; Macromedia, San Francisco, CA). Tokens (6 actors $\times$ 5 tones of voice) were presented 5 times in random order (total of 300 stimuli divided in 2 equivalent blocks of 150) to 12 participants (6 males and 6 females), neither of whom participated in the experiment. They were instructed to label each token with one of the five emotion labels. Mean recognition rates for happy

Abbreviations: fMRI, functional MRI; SPM, statistical parametric map; SVC, small volume collected.

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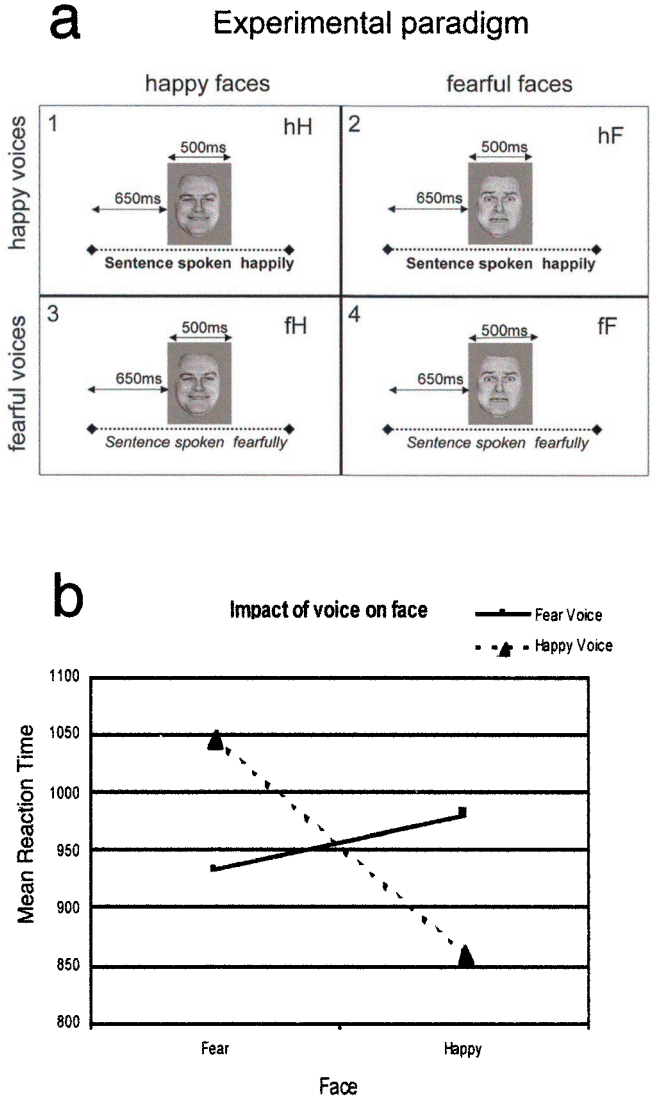

Fig. 1. (*a*) Experimental design. Subjects viewed either happy or fearful faces while listening to sentences spoken in either happy or fearful tones. There were four resulting conditions: (*i*) congruent happy face, hH; (*ii*) incongruent fearful face, hF; (*iii*) incongruent happy face, fH; and (*iv*) congruent fearful face, fF. Subjects were instructed to identify faces as either happy or fearful (by means of a button press) but to disregard to the accompanying voice. The spoken sentence was 2 sec in duration on average, whereas the face was presented for 500 msec. (*b*) Behavioral results. Plots of the mean reaction times (RTs) for categorizing facial expression in all four conditions are shown. Repeated measure ANOVAs with two factors, facial emotion (fear/happy) and congruency with vocal emotion (congruent/incongruent), were carried out on percentage ''fear'' responses and RTs, respectively. For percentage fear, the only significant effect was emotion ($F1, 11 = 129$; $P < 0.001$). For RTs, the effect of congruency fell short of significance ($F1, 11 = 4.49$; $P = 0.058$) by ANOVA, but were significant ($P = 0.05$) by one-tailed t test. The use of one-tailed assessment is justified by the existence of a clear prediction. Thus, subjects had significantly faster responses in the congruent conditions.

tokens were 90% (6% errors because of confusion with neutral and 4% with angry) and 86% correct for fear (8% errors because of confusion with neutral, 4% with sad, and 2% angry). Happy and fear tokens were subsequently selected for use in the present study where recognition rates were in all instances over 80% correct.

Psychological Task. Faces were presented for 0.5 sec (see Fig. 1*a*) with an explicit task instruction to categorize, as quickly and accurately possible, the faces as either fearful or happy. Subjects were instructed to judge the face and ignore the voice. Responses, recorded with respect to speed and accuracy, were made by means of a right-hand button press. In all, there were six individual faces matched with six individual voices. Thus, the experimental design crossed sensory modality (face, voice) with expression (fearful, happy), producing four different event types: happy voice with happy face (hH); happy voice with fearful face (fH); fearful voice with happy face (hF); and fearful voice with fearful face (fF).

fMRI Scanning. We used an event-related fMRI design involving 24 replications of each condition giving rise to a total stimulus number of 96. The four event types were presented in a randomized order. The intertrial interval averaged 3 repetition times (TRs; a single TR being 4.1 sec in duration) with a random jitter of $+/-2.05$ sec. Scanning involved fMRI, using an event-related paradigm. Neuroimaging data were acquired with a 2-T Magnetom VISION whole-body MRI system (Siemens, Erlangen, Germany) equipped with a head volume coil. Contiguous multislice T2*-weighted echoplanar images were obtained by using a sequence that enhanced blood oxygenation level-dependent (BOLD) contrast. Volumes covering the whole brain (48 slices; slice thickness 3 mm) were obtained every 4.1 sec. A T1-weighted anatomical MRI was also acquired for each subject.

Data Analysis. The fMRI data were analyzed by using statistical parametric mapping (SPM 97; refs. 12 and 13; see http://www.fil.ion.ucl.ac.uk/spm). After realignment to the first volume, the functional (T2*-weighted) scans were spatially normalized to a standard template (14, 15). A structural (T1-weighted) MRI, acquired using an MPRAGE three-dimensional sequence ($1 \times 1 \times 1.5$ mm), was coregistered to the functional scans and transformed into the same standard space. The functional data were smoothed by using a 10-mm (full width at half maximum) isotropic Gaussian filter. The evoked hemodynamic responses for the four different stimulus events were modeled as delta functions convolved with a synthetic hemodynamic response function and its temporal derivative in the context of the general linear model (16). All events were time-locked to the onset of the face stimuli.

Specific effects were tested by applying linear contrasts, in a fixed-effects analysis, to the parameter estimates for the canonical hemodynamic response function regressor of each event, resulting in a t statistic for every voxel. The t statistics (transformed to Z statistics), constitute an SPM. Ensuing SPMs were interpreted by referring to the probabilistic behavior of Gaussian random fields (12, 17–19).

The specific hypotheses tested in this study relate to two *a priori* predictions. First, we tested a prediction that crossmodal integration during fear processing would involve the amygdala (9). On the basis of our own previous data, indicating fear-specific influences of amygdala activation on the fusiform cortex during processing of faces (10), we also tested a prediction that crossmodal fear-congruency effects, in a face-processing task, would be expressed in modulation of face-processing regions of the fusiform cortex. To determine how the response to a particular emotional facial expression (i.e., fear) was modulated by the emotional intonation of a concurrently spoken phrase (i.e., fearful or happy), we first calculated the appropriate interaction term (i.e., fearful voice/fearful face–happy voice/fearful face–fearful voice/happy face–happy voice/happy face). However, in addition to voxels specific for fearful-face modulation, the interaction term includes voxels responsive to the overall effect of congruency vs. incongruency (i.e., fearful voice/fearful face + happy voice/happy face − fearful voice/happy face + happy voice/fearful face). To assess specific effects we carried out simple pairwise contrasts. For predicted regions

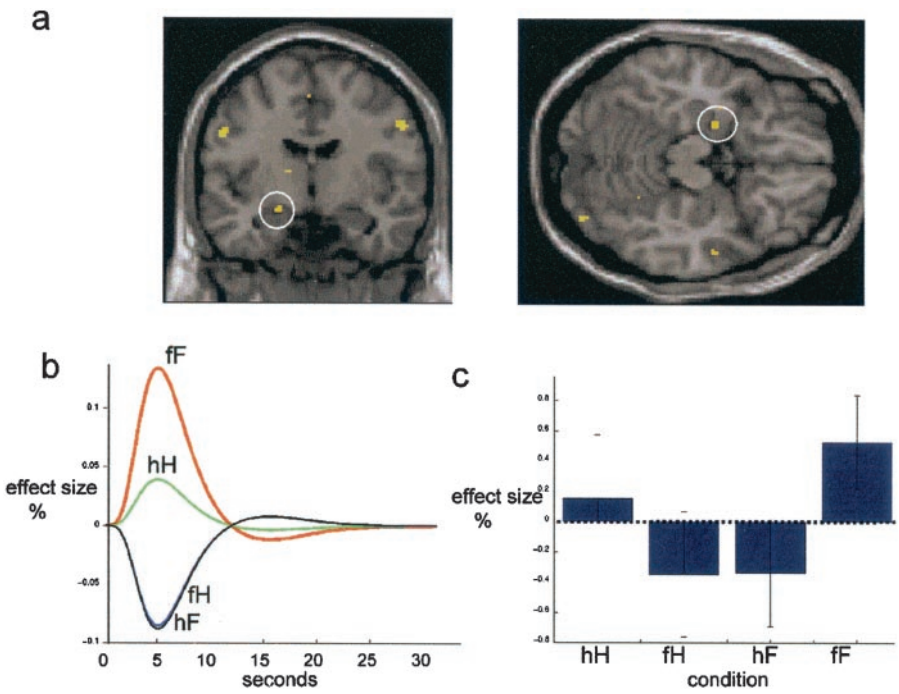

Fig. 2. Amygdala response to congruent fearful voices and faces. (*a*) An SPM showing an enhanced response in the left amygdala to congruent fearful faces (fearful voice + fearful face) compared with incongruent (happy voice + fearful face). The SPM, thresholded at $P < 0.01$ uncorrected, is displayed on coronal and transverse sections of a canonical MRI (derived from the Montreal Neurological Institute) centered on the maximal voxel in the left amygdala ($x = -20$, $y = -6$, and $z = -14$). The left amygdala activation is outlined by a white circle. The bilateral prefrontal activations seen on the display are nonsignificant. Differential responses to congruent happy faces were removed from this contrast by means of an exclusive mask. (*b*) Plots of fitted hemodynamic responses in the left amygdala for all four conditions were derived from above contrast. The baseline of zero is an arbitrary consequence of global scaling, and the apparent decreases for fH and hF conditions are not synonymous with deactivations. (*c*) Parameter estimates of the response for the above contrast in all four conditions from a voxel in the left amygdala ($x = -20$, $y = -6$, and $z = -14$). Note that, as predicted from previous work, a contrast of fF vs. hH conditions alone was significant in each and every subject (conjunction analysis across subjects $P < 0.01$, uncorrected; $x = -12$, $y = -4$, and $z = -18$).

of interest, specifically the amygdala [radius 6 mm based on *a priori* coordinates derived from the Tailarach and Tournoux (14) atlas centered on coordinates x, y, and z (-20, -4, and -14, respectively)] and the fusiform cortex (radius 10 mm and coordinates derived from ref. 20); we used small volume corrections (21). All other reported activations are reported after correction for the entire brain volume sampled. Finally, to test the robustness of individual effects, such as those seen in the amygdala, we carried out conjunction analyses across subjects (22).

Results

Behavioral data collected online indicated significant effects of voice congruency on speed of perceptual categorization of faces (see Fig. 1*b*). Congruency for voice and face was associated with significant response savings, in terms of reaction times (RTs), whereas face–voice incongruency was associated with response costs. Consequently, in simultaneously acquired neuroimaging data we first compared neural responses to presentation of faces in the presence of congruent vs. incongruent emotional voices (hH + fF) − (hF + fH). This contrast revealed significant activation in the left amygdala {x, y, and z [-20, -8, and -14, respectively; $Z = 2.71$; $P < 0.05$, small volume corrected (SVC)]} specific to face processing in the presence of emotionally congruent voices (see Fig. 2*a*). This finding indicates that crossmodal emotional congruency between voice and face leads to augmentation of neural response in the amygdala.

Examination of the parameter estimates for the effects of congruency (see Fig. 2*b*) indicates that the main contributor to the observed effects was derived from the fear congruency (fF) condition. As we were specifically interested in the perceptual bias engendered when a fearful face is viewed in the presence of a fearful voice, we subsequently contrasted the effects of fear congruent (fF) and fear incongruent (hF) face–voice combinations (exclusively masked by hH-fH to remove mere congruency effects). In this contrast, the left amygdala response was significant at the cluster [x, y, and z (-14, 0, and -20, respectively); $P < 0.05$, SVC corrected] and voxel levels [x, y, and z (-20, -6, and -14, respectively); $Z = 2.74$; $P < 0.05$, SVC corrected]. In addition, an activation was also observed in the right fusiform cortex [x, y, and z (30, -62, and -12, respectively); $Z = 3.43$; $P < 0.05$, SVC corrected; see Fig. 3*a*]. Interestingly, activations were also seen in the left anterior cingulate cortex [x, y, and z (0, 32, and 22, respectively); $Z = 3.79$; $P < 0.001$, uncorrected] and both left [x, y, and z (-30, 38, and -12, respectively); $Z = 3.05$; $P < 0.001$, uncorrected] and right orbital prefrontal cortices [x, y, and z (22, 50, and -10, respectively); $Z = 2.92$; $P < 0.01$, uncorrected]. These loci are reported descriptively in view of the fact that all these regions have previously been implicated in emotional processing and were not part of our *a priori* predictions.

To test the robustness of the fear congruency for voice and face seen in the amygdala, we carried out a conjunction analysis, across all 12 subjects, of the contrast of fearful face congruent and incongruent conditions (fF−hF). In this analysis, the effect in the amygdala was significant [two separate peaks at x, y, and z (-26, 2, and -6, respectively); $Z = 3.61$; $P < 0.05$, SVC corrected; and a second peak at x, y, and z (-28, 0, and -10, respectively); $Z = 3.4$; $P < 0.09$, corrected, i.e., showing a strong trend toward significance]. This result indicates that the modulation of the amygdala response by fear congruency was significant in each and every subject.

Finally, we compared the effect of happy face–voice congruency with incongruent combinations (Hh–Hf). In this contrast, activations were noted in the left superior parietal lobule, the left medial parietal cortex, the left superior frontal gyrus, and the right anterior cingulate cortex (all $P < 0.001$, uncorrected). Notably, no effects were seen in the amygdala or in the fusiform cortex, indicating a specificity in these regions for fear-related crossmodal effects.

Discussion

The principal finding in this study is modulation of amygdala and fusiform response to fearful faces when there is emotional congruency in a simultaneously presented voice. Our interpretation of this finding is that it indicates crossmodal integration for the expression of fear in voice and face involves the amygdala and task-specific processing regions of the extra-striate cortex. The finding of modulation in the amygdala is in keeping with a high degree of redundancy for fear processing in this region across different sensory channels. A degree of fear-processing redundancy in the amygdala is supported by neuropsychological

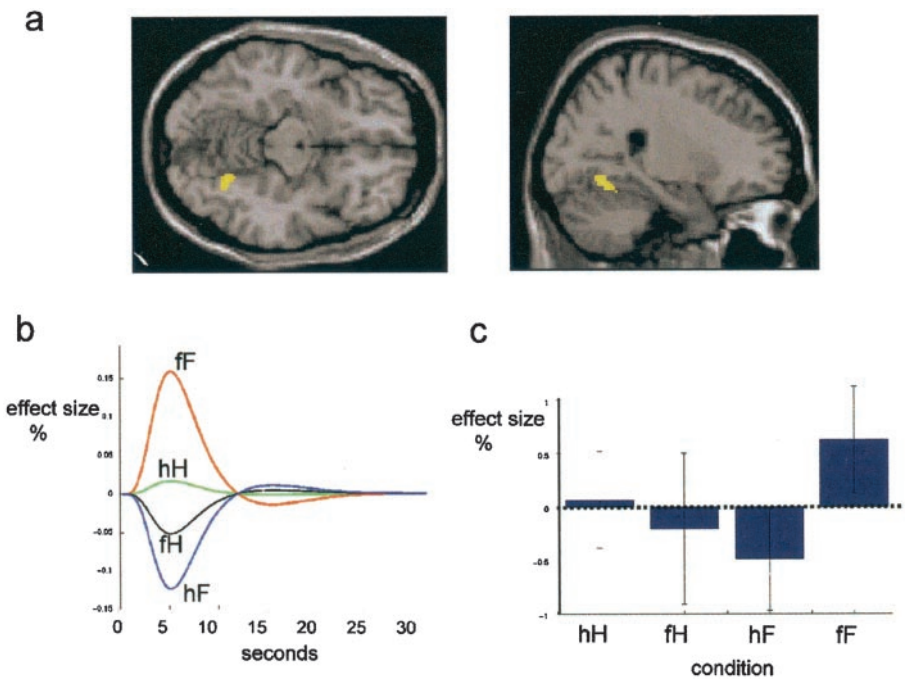

Fig. 3. Fusiform gyrus responses to congruent fearful voice and face. (*a*) An SPM showing an enhanced response in the right fusiform gyrus to congruent fearful voice and face (fF) compared with incongruent happy voice and fearful face (hF). Differential responses to congruent happy voice and face conditions were removed from this contrast by means of an exclusive mask. The SPM, thresholded at $P < 0.01$ uncorrected, is displayed on coronal and transverse sections of a canonical MRI centered on the maximal voxel in the right fusiform gyrus ($x = 24$, $y = -62$, and $z = -10$). (*b*) Plots of fitted hemodynamic responses in the right fusiform for all four experimental conditions at the above coordinates. Note again that the zero value is an arbitrary function of global scaling, and apparent decreases for fH and hF conditions do not correspond to actual deactivations. (*c*) Parameter estimates of the response for the above contrast in all four experimental conditions at the voxel of maximal significance.

studies of patients who have undergone amygdalectomies where fear–face deficits are associated with a symmetrical deficit for fear–voice inputs (23, 24). However, it should be noted that this claim has been challenged by others (25).

Our paradigm involved comparisons between conditions in which there was congruency and incongruency in relation to an expressed emotion. Congruency and incongruency are also important components of the Stroop task, a widely used paradigm in neuropsychological and neuroimaging studies (26). However, there is a crucial difference between these two paradigms. In the Stroop task, the critical behavioral effect is a response cost associated with incongruency, whereas in our paradigm the critical behavioral effect is a response savings associated with congruency (1).

One potential explanation for our findings, that does not invoke crossmodal integration, is that fear congruency conditions engender greater negative affect and this alone accounts for the profile of activation. Our view is that such an explanation is insufficient. First, engendering greater negative affect, when fear is present in both auditory and visual channels, must require emotional integration. Second, although greater negative affect might account for modulation in the amygdala, it is difficult to see how such an explanation accounts for fear-specific modulation in the fusiform cortex. The modulation of fusiform response under the congruency strongly suggests linkage between emotion expressed in the different sensory channels. Note that fear in the voice alone had no effect on the fusiform response to happy faces. Finally, behavioral observations that crossmodal congruency effects can be observed under conditions of divided attention (8), as well as in the absence of awareness of a negative facial affect in prosopaganosic patients (27), argue against an explanation based on the experience of greater negative affect.

The mandatory nature of affective crossmodal effects suggests that the associated neurobiological systems operate independently of attentional control. Indirect evidence that the amygdala can operate preattentively comes from findings of activation to fear-related facial expressions in the absence of stimulus awareness (28, 29). Our finding for involvement of the amygdala specific to fearful voice–face combinations favors an explanation that the amygdala has a key integrative role with respect to emotional content, particularly when that content represents fear or danger, across sensory channels.

The anatomical connectivity of the amygdala provides the necessary architecture to enable crossmodal emotional integration in that it receives inputs, either direct or indirect, from every sensory channel (30, 31). A role for the amygdala in crossmodal sensory processing has been proposed on the basis that surgical extirpations of the amygdala impaired intermodal, but not intramodal, performance on a delay nonmatch to sample (DNMS) task (32). However, subsequent experiments involving neurotoxic lesions to the amygdala failed to find deficits, whereas lesions to the anterior rhinal cortex resulted in major deficits (33). In studies with humans, amygdala damage has failed to result in deficits of intermodal sensory processing (9), although this negative finding was thought to reflect the fact that none of the tasks involved sensory-affective associations. In other words, the critical role proposed by these authors for the amygdala related specifically to emotional crossmodal binding.

In addition to the amygdala, the other finding was modulation of fusiform cortex activation as a function of congruency for fearful voice and face. The locus of modulation falls close to regions of fusiform cortex responsive to presentation of faces (20, 34–36). The modulation we observed is context-specific in that it was expressed exclusively during presentation of congruent fearful face–voice combinations. We have previously observed context-dependent modulation of fusiform cortex activity during presentation of fearful faces, compared with happy faces, expressed as increased connectivity between the amygdala and the fusiform cortex (10), an effect mediated via the extensive back-projection between these regions. In the present experiment, a context-specific enhanced connectivity between the amygdala and the fusiform during congruent voice–face fear processing can account for the observed modulation. However, our current experimental design did not allow assessment of connectivity. The possibility raised by our findings is that a functional consequence of such modulation is an increased perceptual sensitivity to fearful facial expressions. This proposal is in line with recent theoretical suggestions that a consequence of engagement of an emotional system (in the present case, a system involving the amygdala) is enhanced attention and per-

ceptual processing of an emotion-eliciting stimulus (37). Recall that in our experiment the instructions to subjects were to ignore the voice and concentrate on the face stimuli. Although the crossmodal integration is likely to be mandatory and preattentive the specific task instruction, involving selective attention to faces, is likely to account for enhanced perceptual processing in the visual rather than auditory domains during fear congruency conditions.

Our findings indicate that the amygdala has a key integrative role during crossmodal emotional processing. This finding accords with predictions from neuropsychological investigation where the absence of a crossmodal effect was attributed to the lack of behavioral saliency of the stimuli (9). Whether the amygdala alone is sufficient in mediating fear congruency effects or whether its role is to provide access to an extra-amygdala representation of fear cannot be resolved by this study. The modulation of the fusiform cortex indicates that a perceptual biasing effect seen during crossmodal fear processing is an obligatory effect of engagement of a fear representational system.

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