Current Biology, Vol. 13, 2200–2204, December 16, 2003, ©2003 Elsevier Science Ltd. All rights reserved. DOI 10.1016/j.cub.2003.11.049

Seeing Fearful Body Expressions Activates the Fusiform Cortex and Amygdala

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Summary

Darwin's evolutionary approach to organisms' emotional states attributes a prominent role to expressions of emotion in whole-body actions. Researchers in social psychology [1, 2] and human development [3] have long emphasized the fact that emotional states are expressed through body movement, but cognitive neuroscientists have almost exclusively considered isolated facial expressions (for review, see [4]). Here we used high-field fMRI to determine the underlying neural mechanisms of perception of body expression of emotion. Subjects were presented with short blocks of body expressions of fear alternating with short blocks of emotionally neutral meaningful body gestures. All images had internal facial features blurred out to avoid confounds due to a face or facial expression. We show that exposure to body expressions of fear, as opposed to neutral body postures, activates the fusiform gyrus and the amygdala. The fact that these two areas have previously been associated with the processing of faces and facial expressions [5–8] suggests synergies between facial and body-action expressions of emotion. Our findings open a new area of investigation of the role of body expressions of emotion in adaptive behavior as well as the relation between processes of emotion recognition in the face and in the body.

Results and Discussion

In natural situations emotional signals from facial expression, from body posture, and from voice prosody each provide information concerning our emotional states, and together they serve the purpose of adaptive behavior. Given the close relationship between emotional processes and adaptive behavior already pointed out by Darwin [9], it is surprising that only facial expressions have so far been the objects of choice in emotion research [10, 11]. Brain activity directly associated with exposure to body expressions of emotion has not been directly investigated so far. However, there have been some interesting findings in an area that is related to perception of body expressions of emotion. A study of biological motion compared processing of dance-like movements represented by point light displays contrasted with randomly moving dots [12]. The biological movement patterns, which were generally experienced as pleasant, activated subcortical structures including the amygdala. This finding is interesting in view of the important role of the amygdala in processing emotion in facial expressions [7, 13]. It is also consistent with results indicating that the role of the amygdala in emotion processes is not restricted to faces (for review, see [14]). A further finding of related interest is that visual perception of biological motion activates two areas in occipital and fusiform cortex [15]. This result goes in the same direction as the preceding one in the sense that it indicates that areas hitherto best known for processing faces are also involved in processing larger properties typically associated with human bodies. Other recent findings not only indicate a broader role for the amygdala and fusiform cortex than that of processing facial expressions but also provide evidence for close connections between the two areas in the course of processing emotional cues; amygdala activity modulates activation in the fusiform face cortex [16, 17]. Based on these findings, we predicted that the fusiform cortex and amygdala would be areas that selectively activate when subjects are exposed to expressions of fear in the body.

In the present study, we used fMRI to examine the processing of body expressions of fear. Subjects viewed still images of body expressions of fear alternating with emotionally neutral body postures. Selecting meaningful body postures with an emotionally neutral content as a control allowed us to focus specifically on emotion expressed by the body images because both kinds of stimuli involved bodies with some implication of movement. In this first study on body expressions of emotion, we chose not to compare facial expressions and emotional body expressions because of the many differences between these two stimulus classes. For example, implied movement is likely to be a very important dimension of body expressions of emotion, which does not have its equivalent feature in facial expressions, at least not in any of the published brain imaging studies, all of which use static pictures. On the other hand, images of facial expressions have other features, such as direction of gaze, that are not matched by equivalent features of body expressions of emotion. Recent studies make it clear that direction of gaze is an important aspect of facial expressions and determines to some extent how facial expressions are processed [18].

A total of 16 grayscale pictures (eight fearful and eight neutral body postures) were used in an AB-blocked design (Figure 1). The choice of these stimuli was based on the results of a behavioral study in which we investigated how well emotional states could be identified from body expressions (for details, see the Experimental Procedures). Each block lasted 24 s, during which time the pictures were randomly presented for 300 ms followed by 1700 ms of a blank interval, during which only a fixation cross was present. In a second scan, we used an

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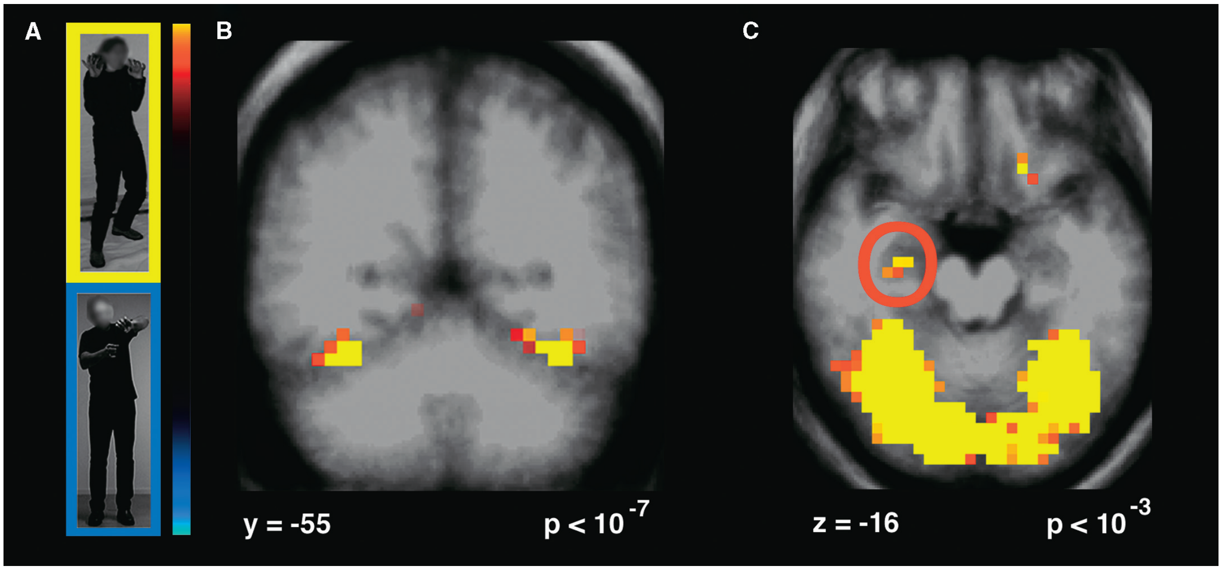

Figure 1. Fusiform and Amygdala Activation in Response to Body Expressions of Fear

(A) Example of the stimuli used. Top: body expression of fear. Bottom: emotionally neutral body posture (pouring liquid in a container). Frame color corresponds to coding on the brain activation map. (B and C) Activation associated with fearful compared with neutral bodies, averaged across seven subjects, in Talairach space. Activation (yellow) can be seen for the fearful bodies in the FFA (A and B) (right: 35; −55; −14. Left: −34; −55; −13) and in the right amygdala (C) (circled in red, 24; 0; −16. No activation is seen for the neutral stimulus [blue]). p values are corrected for multiple comparisons.

independent "face-localizer" to ensure that our region of interest was not only in the fusiform gyrus but also more specifically in the area of the cortex that is reported to be specialized for face perception [5]. This "face-localizer" is similar to that used in [19] and consists of a total of 64 faces alternating with their own Fourier scrambled versions, presented for 1800 ms, followed by a blank interval of 200 ms, all in 24 s blocks. In both experiments, the subjects were instructed to fixate on a central cross during the entire scanning session.

We observed bilateral activation in the fusiform cortex in response to images of fearful bodies compared with neutral ones ($p < 0.0001$). Activation was also observed in the right ($p < 0.001$, corrected for multiple comparisons) amygdala (24; 0; −16). In the left amygdala (−22; 2; −19), activation was also seen but barely reached significance ($p = 0.03$, uncorrected) (Figures 1 and 3).

Further analysis using the region of interest (ROI) defined by our face-localizer test (see Figure 2) and localization of the activation in Talairach space showed that activation in the fusiform gyrus was localized in FFA as described by Kanwisher et al. [5], as well as by several other groups since then (see [20]). (right: 35; −55; −14. Left: −34; −55; −13) (Figure 3).

Previous research indicates that exposure to emotions expressed in the face activates cortical and subcortical structures [4]. For example, the amygdala is sensitive to fearful face expressions [21–24], and its activation is correlated with activity in fusiform and occipital face areas (FFA and IOG) [16]. The fusiform gyrus has been shown to be modulated by emotional faces [16], by emotional scenes [25], and by scenes of high social complexity [26]. Adolphs [6] has also shown that the amygdala is required in order to link the perception of a face to the retrieval of knowledge about its emotional and social meaning. However, in these studies, the stimuli always contained faces, and hence the activation observed in the FFA could be due to the presence of faces. Our stimuli were edited so that no facial expression or facial feature was visible. Hence, the modulation of the FFA that we observed was presumably triggered by body expression of emotion.

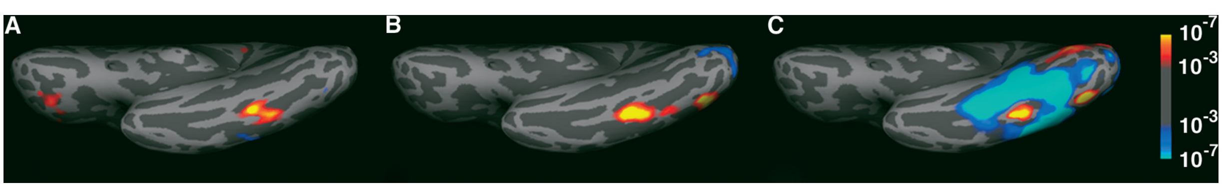

Figure 2. FFA Activation for Body Expression of Fear and for Faces

Ventral view of the right hemisphere of one representative subject: the three panels show FFA activation in three different conditions. Panel (A) shows activation to body expression of fear (face blurred). Panel (B) shows the results of the face localizer we used (faces versus Fourier scrambled version of the faces). Panel (C) shows the results of a comparison between faces (yellow) and objects (blue) (data from [19]). The threshold used ($p < 0.001$, uncorrected) is the same in the three panels; see the logo in the right.

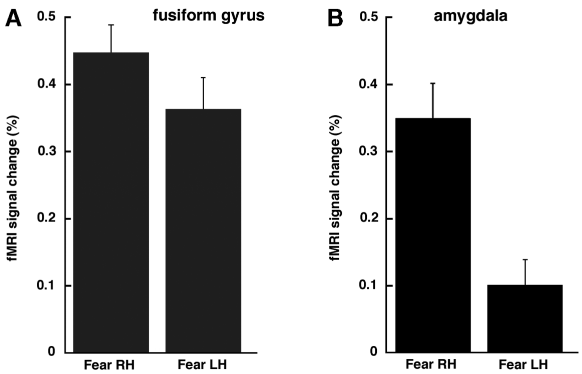

Figure 3. Average Percent Signal Change in FFA and Amygdala

Average percent signal change in (A) functionally defined ROIs in the FFA and (B) amygdala in the comparison between fearful and neutral body postures. The right hemisphere shows more activation than the left hemisphere, but this difference is significant in the amygdala only (FFA: $p = 0.1$; amygdala: $p < 0.001$).

Why does presentation of body expressions of emotion generate a pattern of activity that has so far most often been associated with viewing faces? One explanation could be that the observed activations reflect the role of mental imagery. Previous research has shown that mental imagery neutral faces is sufficient to activate fusiform face-selective areas [27]. Alternatively, together with mental imagery or independently of it, a high-level perceptual mechanism sensitive to semantic factors could provide the facial information missing in the input.

However, although neither an explanation based on mental imagery nor one appealing to semantic factors in high-level perception can be ruled out, these explanations may be too general. Indeed, in the present study the fusiform activity is specifically related to presentation of emotional and not of neutral body postures. The fact that we also observe amygdala activity suggests that what drives the observed activity is a mechanism intimately related to how emotions are perceived in bodies and that this mechanism could be similar to the one postulated for facial expressions, in which amygdala-to-fusiform pathways play a critical role [8, 16]. What we are dealing with here is thus not mental imagery of high-level perception per se. Interestingly, though, in a another study we compared the ERP (event-related potentials) for faces and whole bodies (by using the same stimuli, with the faces blurred, as in the present study), and we observed the same N170 potential known to reflect faces when subjects viewed bodies but not objects (Stekelenberg, R., and B.d.G., unpublished data). Importantly, the time course of the N170 indicates clearly that this similarity between faces and bodies relates to similarities between the two stimulus categories at the stage of visual encoding and is unlikely to reflect top-down influences from semantic content typically associated with processes in the post-300 ms windows, such as P300. Rather, our results raise the interesting possibility that the similarity in neural activity for perceptual filling-in taking place here could in fact be due to synergies between the mechanisms underlying recognition of facial expressions and body expressions.

Darwin [9] was the first to describe in detail the body expressions associated with emotions in animals and humans and proposed several principles underlying the organization of these expressions. In natural situations, a particular body expression is most likely to be accompanied by a congruent face expression. It is also well known from animal research that information from body expressions can play a role in reducing the ambiguity of facial expression [28]. Moreover, it has been shown that observers' judgments of infant emotional states depend on viewing whole body behaviors more than on facial expressions [29]. A challenging issue for further research is to explore the nature of the synergies between the different means through which an organism expresses its emotional states. In view of the central adaptive function of emotional states, it is unlikely that these synergies result from relatively late and relatively slow semantic processes.

Our data suggest that the FFA and the amygdala, so far mostly associated with facial expression of fear in the recent brain imaging literature, play a broader role in emotion recognition than has been recognized so far. This result opens new perspectives for understanding emotional processes in normal and in clinical populations. Deficits in the recognition of facial expressions have been reported in clinical populations with primary emotional disorders such as depression [30–32], bipolar disorders [33, 34], and autism [35]. They have also been reported in groups of patients suffering from emotional disorders consequent to motor pathologies such as Parkinson's disease [36, 37] or Huntington's disease [38]. An interesting question is whether these conditions affect not only recognition of facial expressions but also that of body expression of emotion and whether the relationship between an individual's ability to express a body emotion and their ability to perceive it is also affected. Our findings provide a link between the functional significance of face and body cues, which hitherto were considered separately.

Experimental Procedures

Stimulus preparation. Video recordings of eight semi-professional actors (four women) were used for stimulus construction. Recordings were made in a sound- and light-controlled studio with a digital camera (SonyDCR-PC3E). Actors performed either emotionally neutral actions or expressed fear with the whole body. A set of standardized instructions was given to each actor. To obtain recordings of neutral body actions, the instructions specified the action to be performed (hair combing, pouring water in a glass, putting trousers on). Similarly, we obtained emotional body actions by providing actors with a familiar scenario (e.g., opening a door and finding an armed robber in front of them) and asking them to show their reaction. The average length of a sequence depicting a specified action was 5 s. The video clips were computer edited, and still images were obtained for use in separate behavioral experiments [39]. Stimulus selection for the present experiment was based on results of a study in which 16 images of male and female actors expressing four different emotions (anger, fear, sadness, and happiness) with the whole body were validated. For this purpose stimuli were presented one by one on a PC screen and shown for 4000 ms with a 4000 ms interval. A total of 192 stimuli were used (4 expressions $\times$ 16 identities $\times$ 3 repetitions). Subjects were instructed to categorize each stimulus in a forced-choice procedure as quickly and as accurately as possible by pressing one of the four response buttons corresponding to the four emotions. Overall correct recognition rate for all 16 fear stimuli was between 100 and 85 percent, (average 94%), out of which the eight highest ranked were chosen (all recognized at 100% accuracy) for the present study.

Functional MR images of brain activity of seven participants (four males) were collected in a 3 T high-speed echoplanar imaging device (Siemens) with a quadrature head coil. Informed written consent was obtained for each participant before the scanning session, and the Massachusetts General Hospital Human Studies Committee approved all procedures under Protocol #2002P-000228. Image volumes consisted of 45 contiguous 3 mm-thick slices covering the entire brain (repetition time [TR] = 3,000 ms, 3.125 mm by 3.125 mm in plane resolution, 128 images per slice, echo time [TE] = 30 ms, flip angle 90°, field of view [FOV] = 20 × 20 cm, matrix = 64 × 64). Each functional run was motion-corrected with AFNI and spatially smoothed with a three-dimensional Hanning filter (Full Width Half Maximum [FWHM] = 6.0 mm). We estimated stimulus effects at each voxel by using an F-statistic to compute the phase of the signal at the stimulus frequency. Resultant statistical maps were displayed in pseudocolor, scaled according to significance, and projected onto the high-resolution anatomical scan slices in native and Talairach space. We performed a group analysis was performed, based on commonly activated voxels in Talairach space, by constructing anatomically based group averages for each condition.

The functionally defined FFA was used for each subject as an ROI in which activation for emotional body expression was then computed. Raw time courses were extracted from the ROI, normalized, and averaged, and a difference between the means and a two-tailed unpaired t test was computed for fearful versus neutral expressions.

Acknowledgments

This work was supported by the National Institutes of Health (RO1 NS44824-01 to N.H.) and by the National Center for Research Resources (P41RR14075) and the Mental Illness and Neuroscience Discovery (MIND) Institute. We thank Martijn Balsters, Ilja Frissen, and Josh Snyder for their precious technical help as well as all the subjects who volunteered to participate in the experiments.

Received: September 4, 2003
Revised: October 13, 2003
Accepted: October 27, 2003
Published: December 16, 2003

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