Research report

The amygdala encodes level of perceived fear but not emotional ambiguity in visual scenes

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HIGHLIGHTS

- Amygdala activity was modulated by perceived fear intensity.
- Amygdala activity varied proportionally with subject arousal ratings.
- Amygdala activity in complex visual scenes was not modulated by emotional ambiguity.
- Increased insula activity was found for stimuli with greater emotional intensity.
- Amygdala contributions to emotional evaluation extend beyond disambiguating stimuli.

ARTICLE INFO

ABSTRACT

There are two current models of amygdala functioning with regard to identification of emotional expression. Classic models propose that the amygdala contributes to emotional expression recognition and empathy by encoding the level of threat or distress, and as such, responds greatest to more potent fearful cues. However, recent evidence suggests that the amygdala directs attention to relevant object features to disambiguate the stimulus (e.g., the eyes of a fearful face). The present study used fMRI to investigate amygdala functioning during the perception and identification of emotion in complex visual scenes. Participants later rated the images on levels of fear, disgust and arousal. These ratings were used to identify stimuli that were emotionally-ambiguous, emotionally-discrete, and non-emotional for each individual. A whole-brain and ROI approach was used to identify the nature of the amygdala response to visual scenes. Amygdala activity was associated with higher levels of fear in stimuli and was found to reflect the level of arousal in complex visual scenes. In contrast, no activity was observed that would indicate that the amygdala was modulated by emotional ambiguity when discriminating between fearful and disgusting visual scenes. These results are consistent with models that implicate the amygdala in the evaluation and representation of the intensity of fear, and imply that the functional contribution of the amygdala to deciphering threat in visual scenes likely extends beyond the search for emotionally salient features. The results also suggest that using attention to remedy emotion recognition abnormalities in at-risk populations with amygdala dysfunction may not address all key deficits associated with contributions of the amygdala to emotion and empathy.

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1. Introduction

Currently, there are conflicting models concerning the functional contribution of the amygdala to emotional expression identification, and consequently, to emotional empathy. There is now considerable evidence that although the amygdala responds to a number of emotional expressions, it is particularly important for deciphering or representing fear-related stimuli [1,2]. In one view, the amygdala contributes to emotional expression recognition and empathy by encoding the level of threat or distress [3,4]. According to this model, fear-related stimuli act as reinforcers that activate the amygdala, and greater activity is expected for more potent (i.e., less ambiguous) fearful cues. This view is supported by evidence from neuroimaging studies suggesting that the amygdala responds in a graded fashion to fearful facial expressions of variable intensity [5,6]. However, more recently, an alternate model of amygdala function has been proposed. According to this model, the amygdala

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does not encode the level of distress, but rather, directs attention to relevant object features (the eyes in the case of fearful faces) to disambiguate the stimulus [7]. According to this and related models, greater amygdala activity is predicted for more ambiguous stimuli, where ambiguous stimuli are those that have more than one potential meaning, or whose meaning requires greater examination of contextual cues to decipher [7,8]. This model predicts that once attention is directed to the relevant stimulus features, the amygdala is no longer necessary for emotion recognition. Support for this account comes from a study involving SM, a patient with focal bilateral amygdala lesions and severe fear recognition deficits. Adolphs and colleagues [9] showed that SM failed to attend to the eye region of fearful faces, something that controls do readily. Strikingly, once SM received explicit instructions to attend to the eyes, her fear recognition deficit was reversed. A similar attention-related reversal of fear recognition deficits has also been observed in children with callous and unemotional traits [10], a disorder characterized by reduced amygdala activation to fearful faces [11,12]. Also in line with this view, we have recently demonstrated that healthy individuals showed enhanced amygdala activity to fearful faces that had the eyes occluded relative to when the eyes were isolated [13]. Lastly, amygdala activity has also been specifically linked with promoting reflexive gaze shifts toward the eyes when initial fixation is on less diagnostically relevant features [14].

At present, the relationships between the two putative roles of the amygdala for processing fear (intensity encoding versus directing attention to resolve ambiguity) are unclear, as are the contexts in which each role is expressed. In particular, it is unknown whether the amygdala's putative role in deciphering emotion in facial expressions extends to deciphering emotional ambiguity in more complex visual scenes. For example, is the amygdala involved in directing attention to emotionally relevant stimulus features (other than human eyes) when resolving emotional ambiguity in complex visual scenes? Although uncertainty and ambiguity can arise in multiple ways, in the current study we were particularly interested in determining the potential role of the amygdala in deciphering *emotional ambiguity* in complex visual scenes. The examination of amygdala responsiveness to scenes is an important question given that real world emotional stimuli are very rarely encountered in isolation, but instead, within a complex and often cluttered visual environment. Participants examined visual scenes that varied in terms of the degree to which they were characterized as disgusting and fear-related (based on both normative data and individual subject ratings). Participants then made a forced choice determination of whether the emotional quality of the picture was best described as fearful, disgusting, or neutral. Participants later rated the same pictures on dimensions of fear and disgust, allowing us to determine which images were ambiguously versus unambiguously fearful or disgusting for each participant. We reasoned that if the amygdala is particularly involved in deciphering emotional ambiguity in complex scenes, then activity would be highest for stimuli that featured similar levels of fear and disgust (for which more information is likely required to classify them) irrespective of whether the intensity was moderate or high. In contrast, if the amygdala encodes the level of fear or threat depicted in a visual scene, then activity should be greatest in response to images that elicited the highest ratings of fear irrespective of the level of ambiguity. The present study tested these predictions.

2. Methods

2.1. Subjects

Eighteen healthy human subjects (9 male, 9 female) with a mean age of 20.3 (range 16–24, SD 1.97) participated in this experiment. Participants had normal hearing, normal or corrected-to-normal vision, were fluent English speakers, and were without history of neurological or psychiatric illness. The study was approved by the Health Science Research Ethics Board at the University of Western Ontario.

2.2. Stimuli

Forty pictures were chosen from the *International Affective Picture System* (IAPS; [15]) stimulus set that varied categorically on dimensions of fear and disgust, as defined by standardized ratings [16]. Of these stimuli, ten images were chosen as representative of each of four categorical denominations: (1) high fear and high disgust (mean fear = 3.04, mean disgust = 3.23), (2) high fear and low disgust (mean fear = 3.26, mean disgust = 1.81), (3) low fear and high disgust (mean fear = 1.85, mean disgust = 4.78) and (4) neutral stimuli (see Table S1 in Supplementary Materials for complete ratings). Because we were interested in determining the impact of disambiguating stimuli irrespective of the presence of eyes, images were selected that minimized the amount of human eyes present. Thus, in each stimulus category, the number of eyes present ranged from 1 to 2 (per 10 stimuli). An ANOVA was conducted to confirm that there were no significant differences in the number of human eyes present in each category ($F(1, 39) = 0.077$, $p > 0.10$), ensuring that amygdala activity could not be driven by salient facial features.

2.3. Procedure

In this event-related fMRI study, participants completed three runs of a visual emotional identification task (Fig. 1a). All experimental tasks were programmed using E-Prime software [17]. Within a run, each trial began with the presentation of a fixation cross (4000–5000 ms) followed by the presentation of an IAPS image of variable emotional content (3000 ms). Participants indicated with a button press whether the presented image was best characterized as fearful, disgusting, or neutral in nature as quickly and accurately as possible. The order in which the response options appeared was pseudo-randomized across subjects. In each run, participants viewed each of the 40 IAPS images in random order. Additionally, there were 12 'jitter' trials, consisting of a static fixation cross, incorporated into each run, for a total of 52 trials per run. Participants completed 3 runs of the task for a total of 156 stimuli.

2.4. Affective stimulus ratings

Immediately following the scanning session, participants completed an additional emotional rating task to acquire idiosyncratic responses to the stimuli (Fig. 1b). Outside the scanner, participants were presented with an identical stimulus set to that used during the scanned task. For each trial, participants viewed a single picture and rated the extent to which it was arousing, disgusting and fearful. Images were presented at random. During each presentation, participants rated the emotional quality by way of a 7-point Likert scale. A separate Likert scale was presented for each emotional quality rating, and the order in which the emotional ratings (fear, disgust, arousal) were given were randomized on each trial to prevent order effects. Participants were afforded as much time as they deemed necessary to accurately rate the image. For the analysis, each individual subject's ratings were transformed to z-scores, and then classified according to their unique emotional appraisal of the image. This resulted in the creation of five separate categorical divisions: (1) High Fear/High Disgust (HFHD), (2) High Fear/Low Disgust (HFLD), (3) Low Fear/High Disgust (LFHD), (4) Medium Fear/Medium Disgust (MFMD), and (5) Low Fear/Low Disgust (LFLD; see Fig. S1 in Supplementary Materials for an illustration of the distribution of how subjects categorized the stimuli). In addition, the ratings gleaned from the subjects were used in a continuous fashion to allow us to complete an individualized amplitude modulated analysis of the neuroimaging data (described below).

2.5. Imaging

2.5.1. MRI data acquisition

Subjects were scanned during the task using a 3 T Siemens Scanner with a 32 channel head coil. fMRI images were taken with a T2*-gradient echo-planar imaging sequence (repetition time [TR] = 2500 ms, echo time [TE] = 36 ms; field of view [FOV] = 19.6 cm, 98 × 98 matrix). Scan parameters were chosen that would optimize the signal-to-noise ratio for the amygdala based on recent recommendations in the literature [18,19]. These included smaller voxel sizes and an adjusted TE. All scanner images were acquired during a single scanning session. For all functional runs, complete brain coverage was obtained with 34 interleaved slices of 2.0 × 2.0 mm in plane with slice thickness of 2.0 mm, forming 2.0 mm isovoxels. A series of 140 functional images were collected for each run. A high resolution T1 weighted anatomical scan was obtained prior to fMRI acquisition and covered the whole brain (TR = 2300 ms, TE = 4.25 ms; FOV = 25.6 cm, 192 axial slices; voxel size = 1 mm isovoxels; 256 × 240 matrix) in both scan sessions.

2.5.2. fMRI analysis

Analysis of the fMRI data was conducted using Analysis of Functional NeuroImages (AFNI) software [20] for both the individual and group levels. Motion correction was performed by registering all volumes to the relevant functional volume acquired