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Brain and Cognition 61 (2006) 243–248
Brain and Cognition
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Amygdala activation during masked presentation of emotional faces predicts conscious detection of threat-related faces

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Accepted 20 January 2006
Available online 28 February 2006

Abstract

It has been argued that critical functions of the human amygdala are to modulate the moment-to-moment vigilance level and to enhance the processing and the consolidation of memories of emotionally arousing material. In this functional magnetic resonance study, pictures of human faces bearing fearful, angry, and happy expressions were presented to nine healthy volunteers using a backward masking procedure based on neutral facial expression. Activation of the left and right amygdala in response to the masked fearful faces (compared to neutral faces) was significantly correlated with the number of fearful faces detected. In addition, right but not left amygdala activation in response to the masked angry faces was significantly related to the number of angry faces detected. The present findings underscore the role of the amygdala in the detection and consolidation of memory for marginally perceptible threatening facial expression.

Keywords: Emotion recognition; Facial expression; Amygdala; Functional magnetic resonance imaging; Threat

1. Introduction

The amygdala is a brain structure located in the medial temporal lobe and known to be involved in the recognition of emotionally valenced stimuli (Adolphs, 2002; Rolls, 1999). Results from early functional neuroimaging studies indicate that the amygdala has a central role in the processing of threat-related facial expression, especially of fearful faces (Morris et al., 1996). Evidence was found that the amygdala responds to fearful faces even when processing them outside conscious awareness (Whalen et al., 1998; Williams, Morris, McGlone, Abbott, & Mattingley, 2004). These automatic processes are assumed to be mediated primarily through a short-latency pathway from the sensory thalamus to the amygdala (LeDoux, 1996). In a series of recent neuroimaging studies it was observed that the amygdala is also involved in the processing of happy, sad, and angry facial expression (Breiter et al., 1996; Wright, Martis, Shin, Fischer, & Rauch, 2002; Yang et al., 2002), even when the faces are presented below the level of conscious awareness (Killgore & Yurgelun-Todd, 2004; Nomura et al., 2004).

According to Whalen (1998) the amygdala should be considered an integral component of a constant vigilance system that is preferentially invoked during the perception of ambiguous stimuli of biological relevance such as facial emotions. Fearful faces provide information about the presence of threat but give little information about the source or location of that threat. Angry faces provide information about the source of the threat, but an angry face must not necessarily indicate an impending attack towards the observer. Happy facial expression normally indicates something positive but can, for example in case of an enemy, also signal that something negative is going to happen to the observer. Thus, to fully understand the biological relevance of facial emotions an observer needs additional context information. Data from animal research suggest

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doi:10.1016/j.bandc.2006.01.005

that, immediately after the amygdala responds to a relevant stimulus, cortical neurons will demonstrate lower thresholds for the detection of subsequent sensory information (Kapp, Wilson, Pascoe, Supple, & Whalen, 1990). It has been therefore hypothesized that, in the presence of a masked emotion face, cortical thresholds for detecting sensory stimuli are lowered, and previously undetected stimuli would be noticed (Whalen, 1998). There is evidence that lesions of the human amygdala reduce the likelihood of marginally perceptible emotional stimuli reaching awareness (Anderson & Phelps, 2001). Nomura et al. (2004) observed a positive correlation of the activation of the amygdala in response to masked angry faces and judgment of anger (in rather neutral) target faces suggesting a subtle biasing or modulation function of the amygdala over the overt recognition process.

Converging findings of animal and human studies provide strong evidence that the amygdala is also critically involved in the acquisition and the retaining of memories of emotional experiences (see, e.g., Cahill, 2000; McGaugh, 2002, 2004, for reviews). Several functional brain imaging studies have shown that amygdala activity during encoding relates to long-term memory for emotionally arousing material but not to memory for emotionally neutral material (e.g., Cahill et al., 1996; Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000; Hamann, Ely, Grafton, & Kilts, 1999). These studies support the "memory-modulation" hypothesis of amygdala function by showing a selective role for the amygdala in enhanced memory for emotional stimuli. Recently, Kilpatrick and Cahill (2003) using structural equation modeling of PET scans found evidence for an amygdala modulation of parahippocampal and ventrolateral prefrontal regions during emotionally influenced memory storage. Both of these brain regions are known to be involved in memory storage processes (e.g., Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998; Wagner et al., 1998).

Backward masking procedures are used to investigate non-conscious automatic mechanisms of stimulus analysis. With these procedures, the conscious recognition of a target stimulus is blocked by an immediately following masking stimulus. The stimulus onset asynchrony (SOA) between target and mask appears to be the principal factor influencing recognition of masked facial emotion expressions (Esteves & Öhman, 1993). Conscious awareness of briefly shown emotional faces can be prevented by the use of neutral facial expressions as masking stimuli when SOAs are <40 ms (Esteves & Öhman, 1993).

In the present fMRI study we examined whether a high activation of the amygdala during the masked presentation of facial emotions is associated with a conscious detection of these facial expressions. It was hypothesized that the activation of the amygdala during the processing of marginally perceptible angry facial expression will correlate positively with the number of angry faces detected and the activation of the amygdala during the processing of marginally perceptible fearful facial expression will correlate positively with the number of fearful faces detected. It has been argued (Davis & Whalen, 2001) that the amygdala shows greater activation to a stimulus, the more ambiguous and threatening it is. Thus, provided that the amygdala is involved in the lowering of the perceptual threshold, fearful facial expressions can be expected to be detected more frequently than angry or happy facial expressions.

2. Method and procedure

Nine healthy right-handed volunteers (7 women and 2 men, mean age = 22.3 years, $SD = 2.1$) participated in this functional magnetic resonance study (fMRI) study. Handedness was defined by the Handedness Questionnaire (Raczkowski, Kalat, & Nebes, 1974). The subjects, all of whom were naive with regard to the hypotheses of the experiment, were told that they would see pictures of faces and that they should memorize them. They all gave written informed consent to the experiment, which was approved by the institutional ethics committee. All subjects had no history of psychiatric or neurological illness, were free of psychotropic medication, and had normal or corrected-to-normal vision. The DIA-X interview (Wittchen & Pfister, 1997), a standardized psychiatric screening interview, was administered to assess current and past psychiatric symptomatology.

Face stimuli consisted of fearful (F), angry (A), happy (H), and neutral (N) expressions of 10 individuals (Ekman & Friesen, 1976) which had undergone computer gray-scale normalization. Thus, 40 pictures were used in the fMRI experiment. All photographs were presented repeatedly.

Subjects were presented with alternating 30 s epochs of masked fearful, masked angry, masked happy, and neutral faces or a no-face control stimulus (a gray rectangle). Within epochs, masked stimuli were presented twice per second in a random sequence. Each trial had a duration of 500 ms. In masked face trials a fearful, angry, or happy expression was presented for 33 ms, followed immediately by a 467 ms neutral expression. In non-masked face trials neutral facial expression was shown for 500 ms. The no-face control stimulus was shown for 450 ms followed by a blank screen for 50 ms.

The order of the 30 s epochs containing facial stimuli was counterbalanced across subjects. There were four counterbalanced orders of presentation (Latin square design) [1. c (no-face control epoch), A, c, F, c, H, c, N, c, A, c, F, c, H, c, N; 2. c, F, c, N, c, A, c, H, c, F, c, N, c, A, c, H; 3. c, N, c, H, c, F, c, A, c, N, c, H, c, F, c, A; 4. c, H, c, A, c, N, c, F, c, H, c, A, c, N, c, F]. Thus, each face epoch was preceded by a no-face control epoch and was presented twice, so that the overall presentation time was 8 min.

In a first investigation face stimuli of Ekman and Friesen (1976) were presented to an independent sample (10 females and 10 males; age M, 28.4 years; SD, 8.4 years) with the task to identify the emotional quality of the masked faces. In this experiment masked faces were presented for 33 ms, followed immediately by a 333 ms neutral expression. The mean sensitivity index d' of study participants