

Effects of Gaze on Amygdala Sensitivity to Anger and Fear Faces

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The amygdala is thought to be part of a neural system responsive to potential threat (1). Consistent with this is the amygdala's well-documented sensitivity to fear faces. What is puzzling, however, is the paucity of evidence for a similar involvement of the amygdala in the processing of anger displays. To address this apparent anomaly, researchers have speculated that the amygdala is involved not only in detecting threat but also in deciphering the source of threat, particularly when it is ambiguous (2). Virtually all studies to date investigating facial affect have used only direct-gaze facial displays. The issue of gaze becomes pertinent because anger faces signal impending aggression on the part of the expressor, whereas fear faces indicate potential environmental threat perceived by the expressor. Thus, when coupled with direct gaze (i.e., eye contact with observer) anger faces should indi-

plished with direct gaze and fear faces coupled with averted gaze are recognized more quickly and accurately than either anger faces coupled with averted gaze or fear faces coupled with direct gaze (3). Thus, by manipulating the gaze direction of anger and fear displays, the current study examined the role of the amygdala in processing threat-related ambiguity. Because of the amygdala's demonstrated separate involvement in gaze direction and facial expression processing (4, 5), we identified this brain structure as particularly likely to be involved in their combined processing.

We used functional magnetic resonance imaging (fMRI) to test whether amygdala sensitivity to anger and fear displays would differentially vary as a function of gaze direction (6). Specifically, anger faces coupled with averted gaze and fear faces coupled with direct gaze (ambiguous

ed interaction, however, was found in the left amygdala, $F(1,10) = 5.39$, $P < 0.05$ (Fig. 1).

By merging the study of facial expressions with the study of gaze direction perception, the current research demonstrates an important interaction of these cues on amygdala functioning. This interaction highlights a role for the amygdala in discerning not only the presence of facially communicated threat but also in processing threat-related ambiguity. Consequently, this finding offers an explanation for why previous work has often failed to detect amygdala responsivity to anger displays, and it underscores the importance of incorporating gaze direction in future work on facial expression perception.

References and Notes

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6. Eleven participants (8 male) categorized the gender of randomly presented faces displaying anger or fear coupled with direct or averted (left or right) gaze (fig. S1). Stimuli were back-projected onto a screen for viewing inside the MRI. A total of 30 exemplar faces (15 female) were randomly presented twice in each condition for a total of 120 trials in an event-related design. Sixty trials of low-intensity joy were also included to avoid habituation effects. Stimuli were preceded by a 500-ms fixation cross and remained on screen for 2000 ms. Functional images were acquired in a 1.5T GE Signa system using a gradient echo-planar T2*-sequence sensitive to blood-oxygenation level-dependent (BOLD) contrast. Image volumes consisted of 25 noncontiguous slices (4.5 mm thickness, 1 mm gap, 64 by 64 matrix, repetition time = 2.5 s, TE = 40 ms, flip angle = 90°, field of view = 24 by 24 cm) covering the whole brain. All images were corrected for slice timing, realigned, coregistered, normalized, and smoothed (4 mm full-width at half-maximum) using default parameters in SPM99. Our analyses were restricted to the left and right amygdalae based on contrasts between fear and baseline (average activation of voxels) using random-effects models in SPM99 (height: $P < 0.01$, uncorrected; extent: 5 voxels). The data were examined for the presence of sex of participant effects and none were found.
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Supporting Online Material

www.sciencemag.org/cgi/content/full/300/5625/1536/DC1
Fig. S1

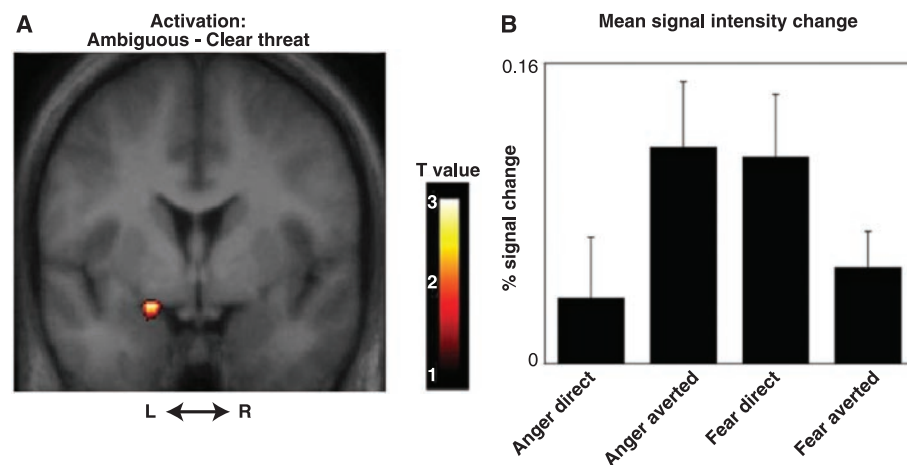


Fig. 1. Amygdala response to emotional facial displays with direct and averted gaze. (A) Activation associated with contrast ambiguous threat (anger/averted and fear/direct) minus clear threat (anger/direct and fear/averted) ($P < 0.01$, uncorrected; left: $-15, 0, -18$). (B) Corresponding mean BOLD signal intensity changes in left amygdala during presentation of angry and fearful faces as a function of direct and averted gaze.

cate more clearly that threat is directed at the observer, whereas when coupled with averted gaze (i.e., laterally shifted gaze) fear faces should indicate more clearly where in the environment that threat is located.

Consistent with these claims, recent research demonstrates that gaze direction differentially modulates the perceptual clarity of anger and fear facial displays. Anger faces cou-

pled with direct gaze and fear faces coupled with averted gaze were predicted to elicit stronger amygdala responses than anger faces coupled with direct gaze and fear faces coupled with averted gaze (clear threat) (Fig. 1). To examine this relation, a two-by-two analysis of variance (anger/fear versus direct/averted gaze) was computed. Activation in the right amygdala was not found to differentially vary in response to anger and fear faces as a function of gaze direction. The predict-

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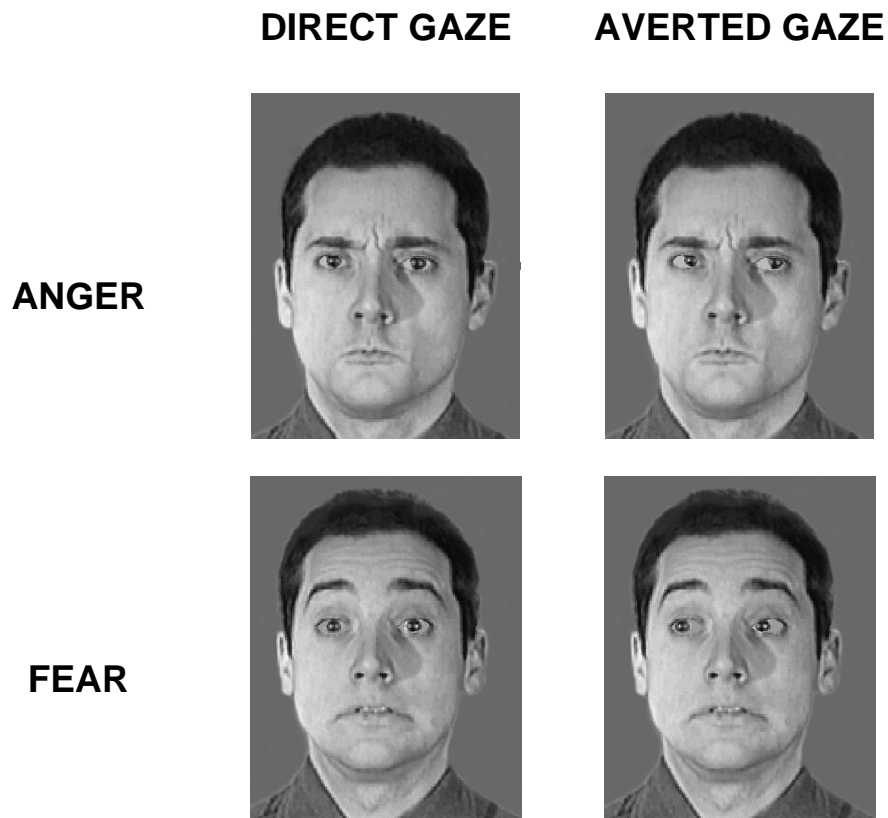


Fig. S2. Example stimuli. **(Above)** Exemplar face, taken from the Montreal Set of Facial Displays of Emotion developed by M.G. Beaupré, N. Cheung, and U. Hess, depicting example facial display within each treatment condition. Gaze direction was manipulated using Adobe Photoshop™. Additional stimuli were selected from the Pictures of Facial Affect developed by P. F. Ekman and W. V. Friesen, the Young Adult Facial Displays developed by R. B. Adams, Jr. and R. E. Kleck, and a set developed by G. Kirouac and F. Y. Doré.