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Affective learning modulates spatial competition during low-load attentional conditions

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Abstract

It has been hypothesized that the amygdala mediates the processing advantage of emotional items. In the present study, we employed functional magnetic resonance imaging (fMRI) to investigate how fear conditioning affected the visual processing of task-irrelevant faces. We hypothesized that faces previously paired with shock (threat faces) would more effectively vie for processing resources during conditions involving spatial competition. To investigate this question, following conditioning, participants performed a letter-detection task on an array of letters that was superimposed on task-irrelevant faces. Attentional resources were manipulated by having participants perform an easy or a difficult search task. Our findings revealed that threat fearful faces evoked stronger responses in the amygdala and fusiform gyrus relative to safe fearful faces during low-load attentional conditions, but not during high-load conditions. Consistent with the increased processing of shock-paired stimuli during the low-load condition, such stimuli exhibited increased behavioral priming and fMRI repetition effects relative to unpaired faces during a subsequent implicit-memory task. Overall, our results suggest a competition model in which affective significance signals from the amygdala may constitute a key modulatory factor determining the neural fate of visual stimuli. In addition, it appears that such competitive advantage is only evident when sufficient processing resources are available to process the affective stimulus.

Keywords: Attention; Emotion; Fear conditioning; Facial expressions; fMRI

A popular view of visual processing suggests that multiple items compete for limited processing resources (Desimone & Duncan, 1995; Kastner & Ungerleider, 2000). Such competition can be biased by both bottom-up and top-down factors, such as stimulus salience and selective attention, respectively. Whereas directed attention to a stimulus facilitates its processing, both perception and the underlying neural responses of objects outside of the focus of attention are attenuated when attentional resources are consumed (Rees, Frith, & Lavie, 1997). At the same time, the perception of emotion-laden visual stimuli, such as facial expressions and emotional scenes, is thought to be prioritized, and to proceed under some conditions of inattention (Pessoa, 2005; Vuilleumier, 2005). In attempting to understand whether emotional perception depends on attention, investigators often focus on the amygdala, a subcortical structure that is believed to be important for the processing of biologically relevant stimuli (Davis & Whalen, 2001). Differential responses in the amygdala for unattended stimuli (Anderson, Christoff, Panitz, De Rosa, & Gabrieli, 2003; Vuilleumier, Armony, Driver, & Dolan, 2001), as well as for stimuli that subjects are potentially unaware of (Whalen et al., 1998, 2004), are viewed as evidence that emotional perception is “automatic” (Öhman & Mineka, 2001). On the contrary, other studies suggest that emotional perception is, in fact, dependent on attention (Bishop, Jenkins, & Lawrence, 2007; Eimer, Holmes, & McGlone, 2003; Holmes, Vuilleumier, & Eimer, 2003; Hsu & Pessoa, 2007; Pessoa, McKenna, Gutierrez, & Ungerleider, 2002; Pessoa, Padmala, & Morland, 2005; Silvert et al., 2007) and other top-down factors (Ishai, Pessoa, Bikle, & Ungerleider, 2004), as revealed by robust valence by attention interactions in the amygdala (and other brain regions). Because previous studies suggesting that emotional perception depends on attention have employed stimuli that are not strongly arousing (e.g., facial expressions of fear or anger), it is conceivable that the effects of attention (i.e.,

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lack of "automaticity") were due to the usage of "less arousing" emotional stimuli.

To address this possibility, in the present study, we investigated the role of visual attention during the processing of emotion-laden visual stimuli by initially pairing a subset of our emotional faces with mildly aversive electrical stimulation. This form of aversive conditioning is dependent on the amygdala in both non-human species and humans (Davis & Whalen, 2001; Phelps & LeDoux, 2005). During conditioning, a stimulus acquires affective significance (conditioned stimulus, CS+) when paired with an aversive stimulus (unconditioned stimulus, US). We reasoned that such pairing would potentiate the processing of shock-paired faces. For instance, emotional words are less likely to be missed under attentionally demanding conditions (Anderson & Phelps, 2001). Collectively, a body of findings suggests that emotionally salient events are associated with enhanced perception (Vuilleumier, 2005). Overall, one of the goals of our experimental manipulation was to increase the affective significance of visual stimuli, such as facial expressions, commonly employed in studying the interaction between attention and emotional processing (Pessoa, McKenna et al., 2002; Williams, McGlone, Abbott, & Mattingley, 2005).

In the present study, we investigated how fear conditioning affected the visual processing of task-irrelevant faces. We hypothesized that stimuli with increased affective significance would have a competitive advantage relative to other stimuli during conditions involving spatial competition. Because of the role of the amygdala in emotional perception and the role of the fusiform gyrus in the processing of faces (Allison, Puce, Spencer, & McCarthy, 1999; Kanwisher, McDermott, & Chun, 1997), we were particularly interested in evaluating responses evoked in these structures. We tested our hypothesis in two complementary ways, which involved a letter-detection task and a subsequent implicit-memory task. Following an initial conditioning phase, participants performed a letter-detection task on an array of letters that was superimposed on task-irrelevant faces (Fig. 1). Attentional resources were manipulated by having participants perform an easy or a difficult search task. We predicted that faces previously paired with shock would be potentiated, leading to increased resistance to the effects of attention. For instance, fearful faces that were previously paired with shock would be expected to evoke stronger responses relative to unpaired faces in the amygdala and fusiform gyrus during both easy and hard attentional conditions—i.e., fearful faces paired with shock would resist the effects of attention, which in some studies have eliminated emotion-related differential responses (Bishop, Duncan, & Lawrence, 2004; Mitchell et al., 2007; Pessoa et al., 2005; Silvert et al., 2007). Subsequent to the letter-detection task, participants performed an implicit-memory task during which behavioral and fMRI-related priming measures were assessed. We predicted that the initial aversive conditioning of faces would allow them to be better (implicitly) encoded in memory during the letter-detection task relative to faces not paired with shock, even though faces were task-irrelevant during this task. Again, we were particularly interested in probing responses evoked by the amygdala and fusiform gyrus. Overall, our design allowed us to test the hypothesis that affective significance would be linked to increased competitive advantage in two separate ways (i.e., via the letter-detection and implicit memory tasks).

1. Methods

1.1. Subjects

Twenty-nine right-handed subjects (17 male), aged 18–34 years, were recruited. All subjects were in good health with no history of neurological or psychiatric disorders and gave written informed consent, as approved by the Institutional Review Boards of Brown University and Memorial Hospital of Rhode Island. Subjects had normal or corrected-to-normal vision. Eight subjects were excluded from data analysis: five subjects were excluded due to excessive head motion during scanning (>2 voxels); one subject was excluded due to chance performance during both the easy (52% correct) and hard (48% correct) letter-detection trials; two subjects were excluded because of insufficient signal quality in the amygdala (see below).

1.2. Stimuli

Face stimuli were taken from the Karolinska Directed Emotional Faces (KDEF) (Lundqvist, Flykt, & Öhman, 1998), the Ekman set (Ekman & Priesen, 1976), the Ishai-NIMH set (Ishai et al., 2004), and the Nimstim Face Stimulus Set (MacArthur Foundation Research Network on Early Experience and Brain Development). All faces were converted to black and white, and both contrast and brightness were adjusted to maintain consistency across the face sets. Our combined face set consisted of 144 identities (72 males and 72 females): 24

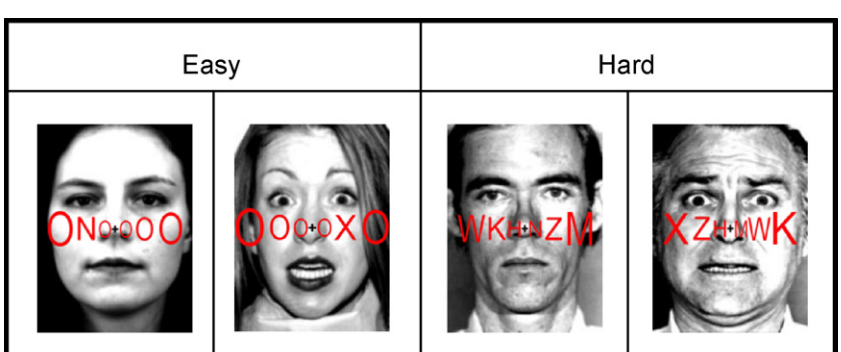

Fig. 1. Sample stimuli used during letter-detection trials. Subjects were asked to report the identity of a target letter (N or X) in the letter array, while ignoring the faces. The easy attentional condition involved the search for a singleton item, while the hard condition involved a more demanding search among a non-uniform set of letters.