Neuropsychologia 47 (2009) 2480–2487

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Affective learning enhances activity and functional connectivity in early visual cortex

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ARTICLE INFO

Article history:
Received 22 December 2008
Received in revised form 20 April 2009
Accepted 24 April 2009
Available online 3 May 2009

Keywords:
Primary visual cortex
Conditioning
Faces
Vision
Emotion
fMRI

ABSTRACT

This study examined the impact of task-irrelevant affective information on early visual processing regions V1–V4. Fearful and neutral faces presented with rings of different colors were used as stimuli. During the conditioning phase, fearful faces presented with a certain ring color (e.g., black) were paired with mild electrical stimulation. Neutral faces shown with rings of that color, as well as fearful or neutral faces shown with another ring color (e.g., white), were never paired with shock. Our findings revealed that fearful faces evoked enhanced blood oxygen level dependent (BOLD) responses in V1 and V4 compared to neutral faces. Faces embedded in a color ring that was paired with shock (e.g., black) evoked greater BOLD responses in V1–V4 compared to a ring color that was never paired with shock (e.g., white). Finally, BOLD responses in early visual cortex were tightly interrelated (i.e., correlated) during an affectively potent context (i.e., ring color) but not during a neutral one, suggesting that increased functional integration was present with affective learning. Taken together, the results suggest that task-irrelevant affective information not only influences evoked responses in early, retinotopically organized visual cortex, but also determines the *pattern* of responses across early visual cortex.

Accumulating evidence shows that the processing of affectively significant visual objects is prioritized (Compton, 2003; Vuilleumier, 2005). Affective stimuli that have dominance in visual awareness (Alpers & Gerdes, 2007; Alpers & Pauli, 2006) are processed faster (Stolarova, Keil, & Moratti, 2006) and are more likely to be processed when only limited resources are available (Anderson, 2005; Anderson & Phelps, 2001). Neuroanatomical connections between orbitofrontal cortex (OFC) and both the ventral and dorsal visual streams (Barbas, 1988, 1995; Carmichael & Price, 1995; Cavada, Company, Tejedor, Cruz-Rizzolo, & Reinoso-Suarez, 2000), as well as projections from the amygdala all along the ventral stream (Amaral, Behniea, & Kelly, 2003; Amaral, Price, Pitkänen, & Carmichael, 1992), suggest that affective brain regions functionally modulate visual processing regions (Barrett & Bar, 2009; Duncan & Barrett, 2007; Lang et al., 1998; Pessoa & Ungerleider, 2004; Vuilleumier, 2005). There is accumulating neuroimaging evidence that objects with affective value receive enhanced visual processing even in early, retinotopically organized cortex (e.g., V1–V4). Both affectively salient images (Lane, Chua, & Dolan, 1999; Lang et al., 1998; Mourão-Miranda et al., 2003) and faces (Büchel, Morris, Dolan, & Friston, 1998; Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004) evoke enhanced blood oxygen level dependent (BOLD) responses in early visual areas. A recent meta-analytic investigation summarizing functional magnetic resonance imaging (fMRI) and PET studies of emotion published from 1990 to 2005 confirmed that visual processing areas are consistently activated in response to affectively potent as compared with neutral stimuli (Kober et al., 2008; see Fig. 2 in Wager et al., 2008).

Recent studies have examined how learning the association between a neutral stimulus and electrical stimulation affects associated responses in early sensory areas more generally. For instance, Li, Howard, Parrish, and Gottfried (2008) reported that pairing an odor with electrical stimulation changed the pattern of activity in primary olfactory cortex and enabled participants to discriminate previously indiscriminable odors. In a related study, Padmala and Pessoa (2008) paired the presence of a near-threshold visual patch with electrical stimulation during an initial conditioning phase. In a subsequent experimental phase, participants were better at detecting the visual stimulus when it was predictive of electrical stimulation, a result that was paralleled by increased signal changes in V1, as well as other retinotopically organized visual areas. Related studies have capitalized on the fine temporal resolution of EEG to address analogous questions (e.g.,Keil, Stolarova, Moratti, & Ray, 2007; Schupp, Junghöfer, Weike, & Hamm, 2003).

However, several properties of the impact of affective learning on early sensory representations remain poorly understood. For instance, in previous studies, the effect of learning on sensory representations was typically evaluated for stimuli that are

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doi:10.1016/j.neuropsychologia.2009.04.023

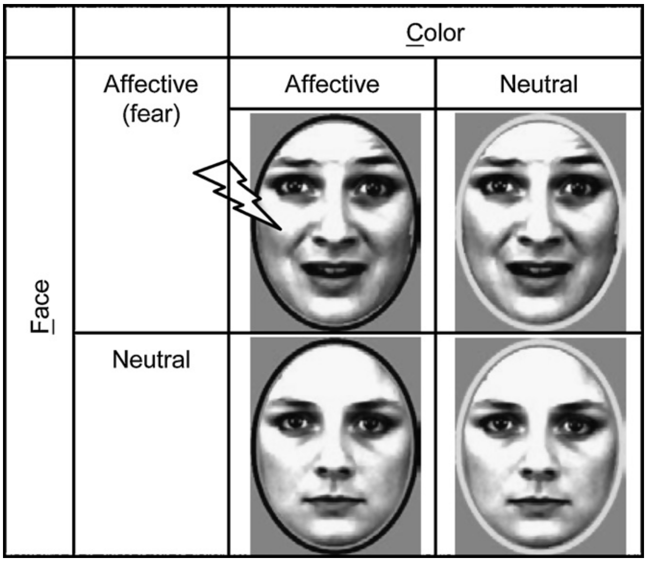

Fig. 1. The experimental design contained four face-ring stimuli combinations. During aversive conditioning, only FaCa faces were paired with mild electrical stimulation; the other three stimuli were never paired with shock. FaCa: face affective, color affective; FaCn: face affective, color neutral; FnCa: face neutral, color affective; FnCn: face neutral, color neutral.

both task relevant and explicitly attended. Here, we reasoned that, like intrinsically affective stimuli (e.g., fearful face), learned affective stimuli would impact visual processing even when the stimuli are task-irrelevant and unattended, at least if processing capacity is not exhausted by the main task (Pessoa, McKenna, Gutierrez, & Ungerleider, 2002). It also remains unclear how learning the association between *compound* stimuli and electrical stimulation impacts evoked responses in early visual cortex. For instance, if a learned stimulus is defined in terms of a conjunction of features, is the impact on early visual responses specific to the conjunction of those features? To investigate these questions, subjects viewed faces depicting neutral or fearful expressions that were surrounded by either a black or a white ring while undergoing fMRI. During an initial aversive learning phase, fearful faces presented with a certain ring color (e.g., black) acquired additional affective salience via pairing with electrical stimulation (Fig. 1). During a subsequent phase, face-ring compound stimuli were task-irrelevant, and subjects performed a simple letter-detection task at fixation (Fig. 2). Our goal was to evaluate fMRI responses in early, retinotopically organized areas to the four types of face-ring pairs.

Importantly, in addition to investigating evoked fMRI responses in early visual cortex, we were interested in probing the *pattern* of activity across retinotopically organized areas. To do so, we computed the correlations between fMRI responses for early visual areas for different face-ring pairings and then compared the correlation structure to those observed in other brain regions robustly engaged by our task. Overall, the correlational analyses allowed us to probe not only the effects of affective significance on individual visual areas (as described above), but also how the *pattern* of effects varied as a function of facial expression under different ring colors, namely, affective contexts.

1. Methods

1.1. Participants

Twenty-eight (8 male) right-handed subjects ranging in age from 20 to 37 years participated in the study. All participants were in good health with no history of neurological or psychiatric disorders as assessed by a neuropsychiatric interview (MINI) and gave written informed consent, as approved by the Institutional Review Board of Indiana University. Participants had normal or corrected-to-normal vision. Two participants were excluded from data analysis: one participant was excluded due to excessive head motion during scanning (>2 voxels) and the other was excluded due to poor behavioral performance (4 SDs below the average of all participants). Two participants did not participate in the retinotopic mapping session, leaving 24 participants for visual region of interest analyses.

1.2. Stimuli and task design

Face stimuli were taken from the Karolinska directed emotional faces (KDEF), the Ekman set (Lundqvist, Flykt, & Öhman, 1998) and the Ishai-NIMH set (Ishai, Pessoa, Bikle, & Ungerleider, 2004). Only neutral and fearful faces were used in this study. All faces were converted to black and white, and both contrast and brightness were adjusted to maintain consistency across the face sets. Faces were cropped of hair and enclosed in a black or white oval ring as shown in Fig. 2. Presentation software (Neurobehavioral Systems, CA) was used to display the stimuli and record behavioral responses throughout the experiment.

1.3. Procedure

1.3.1. Overview

Participants first completed a *conditioning phase* during which they were presented with fearful faces surrounded by a colored ring (Fig. 1) that were paired with electrical stimulation (face affective, color affective, or FaCa) or not (face affective, color neutral, or FaCn), as well as neutral faces that were similarly surrounded but never paired with electrical stimulation (face neutral, color affective or FnCa; face neutral, color neutral or FnCn). For example, for some participants fearful faces ringed in black were paired with electric stimulation (FaCa), whereas fearful ringed in white were not (FaCn). Color was counterbalanced across participants. During the *experimental phase*, participants attended to the center of a computer screen while face-ring pairings varying in degree of affective salience were presented parafoveally (3.5° from the center of the stimulus to the center of the display). On a separate day, participants completed a retinotopic mapping session to allow the delineation of early visual areas (see below).

1.3.2. Conditioning phase

The conditioning phase employed a 2 facial expression (affective vs. neutral) × 2 color (affective: ring color that was associated with electrical stimulation; neutral: ring color that was not associated with electrical stimulation) experimental design. The participants viewed 34 face-ring pairs during this stage. The face-ring stimuli used in each trial were presented in random order with the constraint that no more than two face-ring stimuli of the same type were presented successively. Thirteen trials contained fearful faces embedded in a ring color that was associated with electrical stimulation (FaCa; participants received electrical stimulation in six of these trials). Seven trials contained neutral faces embedded in a ring color that was associated with electrical stimulation (FnCa; participants did not receive electrical stimulation in these trials). Seven trials contained fearful faces embedded in a ring color that was not associated with electrical stimulation (FaCn). Seven trials contained neutral faces embedded in a ring color that was not associated with electrical stimulation (FnCn). In summary, electrical stimulation was delivered in approximately 50% (6/13) of the displays that contained *both* a fearful face and a specific ring color. The first presentation of each stimulus type not involving shock (i.e., FnCa, FaCn, and FnCn) served as a "habituation" trial; data from these trials were

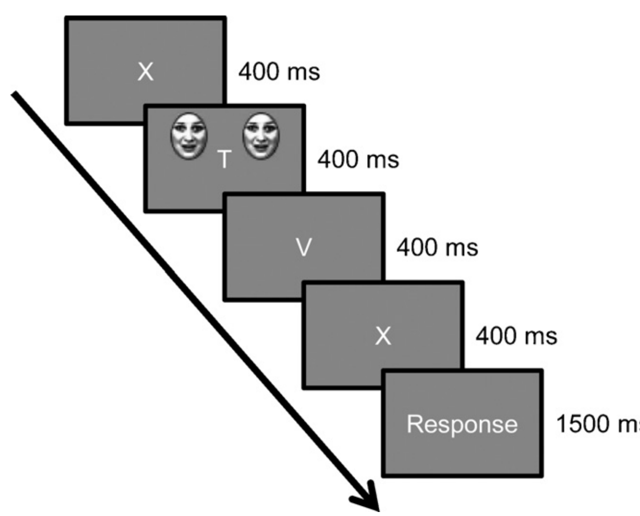

Fig. 2. Trial structure. Participants were asked to report the number of times the target letter "X" was shown in a stream of four letters while ignoring task-irrelevant face stimuli. For clarity, not all trial phases are shown (see text).