Emotion
2008, Vol. 8, No. 1, 96–103

1528-3542/08/$12.00 DOI: 10.1037/1528-3542.8.1.96

Affective Learning Increases Sensitivity to Graded Emotional Faces

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How does the affective significance of emotional faces affect perceptual decisions? We manipulated affective significance by pairing 100% fearful faces with aversive electrical stimulation and hypothesized that increasing the significance of a stimulus via its prior history would lead to enhanced processing. After fear conditioning, participants viewed graded emotional faces that ranged from neutral to fearful. Faces were shown either in a color that was previously paired with shock or a color not paired with shock during conditioning. Increases in the frequency of "fearful" responses for faces shown in the shock-paired color were most robust for faces at intermediate intensity levels (40–60% fearful). Psychometric fits to the data revealed significant increased *sensitivity* for shock-paired relative to unpaired faces. Thus, despite identical physical features for shock-paired and unpaired stimuli (aside from the color, which was counterbalanced), more frequent (and faster) "fearful" responses were made when participants viewed affectively significant stimuli.

Keywords: emotional faces, fear conditioning, skin conductance responses, emotion

Emotional perception is believed to be prioritized (Pessoa, 2005; Phelps, 2006; Vuilleumier, 2005). For example, during fast serial presentations leading to an "attentional blink," emotional words are less likely to be missed than neutral ones (Anderson, 2005). Emotional words are also better identified than neutral ones during a challenging two-choice perceptual task (Zeelenberg, Wagenmakers, & Rotteveel, 2006). Furthermore, recent evidence suggests that many participants are able to detect masked fearful faces even when these are shown briefly for 17 ms (Szczepanowski & Pessoa, 2007). Additional findings also suggest that fearful faces may function as cues that potentiate visual processing (Phelps, Ling, & Carrasco, 2006).

It has been hypothesized that the amygdala mediates the processing advantage of emotional items. For instance, while emotional words are less likely to be missed under attentionally demanding conditions leading to an attentional blink, such competitive advantage is lost in patients with bilateral amygdala lesions (Anderson & Phelps, 2001). Furthermore, in neuroimaging studies, amygdala activation is correlated with activation in visual cortex (Morris et al., 1998; Pessoa, McKenna, Gutierrez, & Ungerleider, 2002) and such modulation is attenuated in patients with amygdala damage—in fact, the extent of visual cortical activation appears to be proportional to the extent of the lesion (Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004).

In the present study, we reasoned that increasing the affective significance of a stimulus via its prior history would lead to enhanced processing. Affective significance was manipulated via fear conditioning, such that a face stimulus acquired increased significance (conditioned stimulus, CS+) when paired with an aversive stimulus (unconditioned stimulus, US). We focused on the following question: How is the perception of a previously conditioned stimulus affected? In particular, can such affective learning affect perceptual decisions? To probe these questions, participants viewed graded faces that varied parametrically in intensity from neutral to fearful and were asked to perform a forced, two-choice task and indicate "neutral" or "fearful." On half of the trials, participants viewed faces shown in a color (red or blue) that had been previously paired with mild electrical stimulation, and on the other half of the trials they viewed faces that had never been paired with shock (shown in the other color). To assess how conditioning affected perceptual decisions, we characterized performance via psychometric curves that related the percentage of "fearful" responses to the intensity of the graded face. In doing so, we were particularly interested in testing a model that has proved important in characterizing the effects of visual attention on behavioral performance and on cell responses in early visual cortex (Carrasco, Ling, & Read, 2004; Reynolds, Pasternak, & Desimone, 2000). The *contrast gain model* predicts that increases in response occur when the intensity of the stimulus is relatively low or intermediate—consistent with a horizontal shift of the psychometric (or neurometric) curve. In the present context, we thus predicted that affective significance would increase *sensitivity* to graded faces, as evidenced by a leftward shift of the psychometric curve relating face intensity and percentage of "fearful" responses (see Figure 1).

Method

Participants

Twenty-six participants between 18 and 40 years of age were recruited. The study protocol was approved by the Institutional Review Board of Indiana University, Bloomington, and participants provided informed consent prior to the experiment. Six

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This work was supported by the NIMH award 1R01 MH071589 to L.P.. We thank Srikanth Padmala for both technical support and conceptual feedback, Paul Krueger for assistance in data collection, and the anonymous reviewers for many insightful suggestions.

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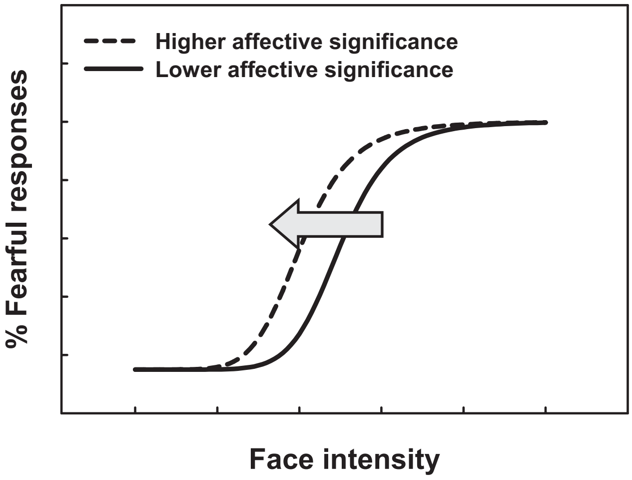

Figure 1. Contrast gain model in the context of our experiment. The *x*-axis represents "face intensity" and the *y*-axis represents "% fearful responses." A leftward shift of the psychometric curve (see arrow) would constitute evidence for increased sensitivity for stimuli with higher affective significance.

participants were excluded from data analysis because they were "nonresponders" as determined during the initial conditioning phase (see below).

Stimulus Materials

Face stimuli were employed from the Karolinska Directed Emotional Faces (KDEF) set (Lundqvist & Litton, 1998), the Ekman Face set (Ekman & Priesen, 1976), and the Ishai-NIMH set (Ishai, Pessoa, Bikle, & Ungerleider, 2004). All stimuli, which were originally black and white, were lightly colored in Adobe Photoshop (Adobe Systems Incorporated, San Jose, CA), such that two sets of faces were employed, one slightly red, one slightly blue. To parametrically vary emotional expression, faces were morphed, generating a sequence of 11 faces ranging from neutral to fearful in 10% increments for each identity (see Figure 2A for examples). Twelve separate identities were employed during the perceptual decision task. Morphing was performed by using the FantaMorph software (Abrosoft, Beijing, China). Face stimuli were presented at the center of the screen and subtended 5.6° × 7.1°.

Conditioning Procedure

In the first phase of the experiment, affective significance was manipulated via fear conditioning. As illustrated in Figure 2B, conditioning was administrated within a 2 (color: shock-paired, unpaired) × 2 (expression: neutral, fearful) structure (the red/blue color used for the shock-paired condition was counterbalanced across participants). During conditioning trials, red or blue 100% fearful faces served as conditioned stimuli (CS+). Thus, the conditioned stimuli involved a combination of *both* facial expression and color (i.e., only 100% fearful faces were paired with shock). As an unconditioned stimulus (US), a 500-ms electric shock (50 Hz) was delivered to the distal phalanges of the third and fourth fingers of the nondominant hand by a shock stimulator (E13-22; Coulbourn Instruments, Allentown, PA). On CS+ trials, faces were followed by a US with a 50% partial reinforcement schedule in a delayed conditioning procedure. Prior to the experiment, participants were instructed of the contingency rule, but they were not informed about the probability of US delivery. The intensity of electric shock, which ranged between 0.8 and 4.0 mA, was determined separately for each participant so as to be "highly unpleasant but not painful."

Conditioning trials proceeded as follows. Following a 500-ms fixation cross, a face was presented for 2 s, followed by a 5.5-s blank screen. On each trial, participants were asked to indicate the color of the face stimulus (red or blue) through button responses. A total of 34 faces were presented in random order: six fearful faces in shock-paired color with shock delivery (CS+ with US); six fearful faces in shock-paired color without shock (CS+); six fearful faces in unpaired color; six neutral faces in shock-paired color; and six neutral faces in unpaired color; four habituation trials (see below). The set of faces employed during conditioning did not overlap with the faces used subsequently during the perceptual decision task.

Skin conductance responses (SCRs) were recorded with the MP-150 system (BIOPAC Systems, Goleta, CA) and Ag/AgCl electrodes placed on the distal phalanges of the index and middle finger of the nondominant (left) hand. SCR was amplified and sampled at 250 Hz and the analysis of waveforms was conducted using AcqKnowledge software (BIOPAC Systems, Goleta, CA). Along with six trials that included US delivery (CS+ with US), four "habituation" trials, defined as the first trial occurrence of each trial type (two colors × two expressions), were excluded from the SCR analysis (such "first" trials were discarded to eliminate "novelty" effects). On each trial, the level of SCR was calculated by subtracting a baseline (average signal between 0 and 1 s) from the peak amplitude during the 1–6-s time window following stimulus onset (Prokasy & Raskin, 1974).

Participants who, during the conditioning phase, did not show differential SCR to CS+ faces (shock-paired, 100% fearful faces) relative to CS- faces (shock-paired, 100% fearful faces) above 0.02 μS were removed from additional analyses (LaBar, Gatenby, Gore, LeDoux, & Phelps, 1998). Their data were not utilized given the lack of evidence of a successful conditioning manipulation.

Perceptual Decision Task

Following the initial conditioning phase, participants performed a forced, two-choice perceptual-decision task (neutral vs. fearful). Participants were encouraged to respond as quickly as possible. Trials were presented in a blocked fashion with the blocks separated from each other by an 8-s fixation condition in which no task was involved (Figure 2C). Throughout a block, all faces were shown in the same color; the color was indicated in an initial 3-s instruction screen. Each block contained 22 trials, shown in random order, in which two face identities were shown for each of the 11 intensity levels. Trials began with a 500-ms fixation cross, which was followed by a face stimulus presented for 100 ms and a mask stimulus for 100 ms. Participants were then asked to indicate whether the face was neutral or fearful via button press. The next trial followed the offset of the face stimulus by 1.8 s. Brief presentations of face stimuli precluded deliberate saccadic eye movements and made the task demanding.

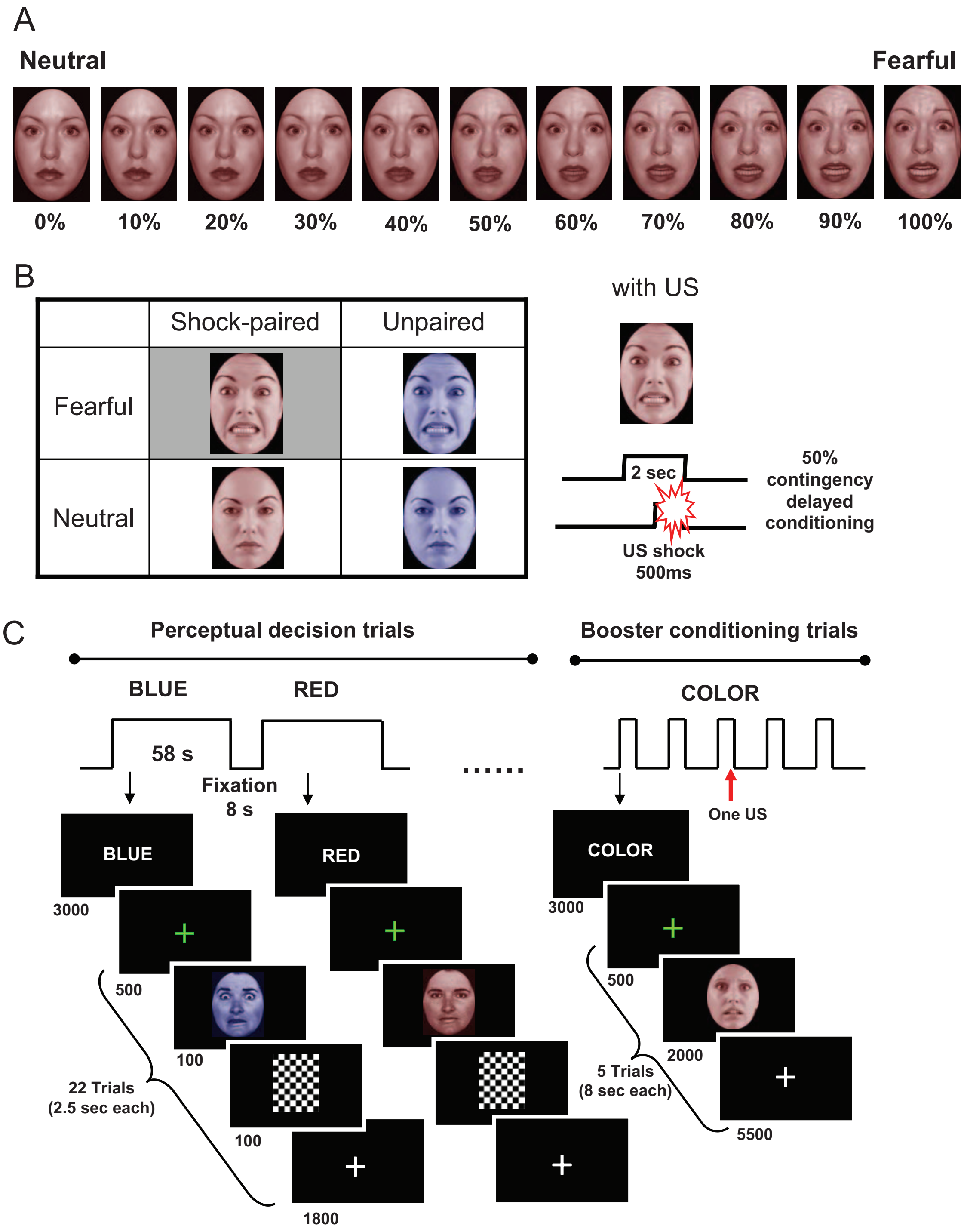

Figure 2. Experimental stimuli and design. (A) Sample face stimuli. Faces ranged from neutral to fearful in 10% increments. (B) The conditioning phase employed a 2 (color) × 2 (expression) structure. Either a red (current example) or a blue, 100% fearful face served as a CS+ stimulus (indicated by the gray background cell), which was paired with shock (US) with 50% probability. (C) Perceptual decision trials followed a "blocked" structure, such that shock-paired and unpaired blocks alternated. During perceptual decision trials, participants were required to indicate "fearful" or "neutral" as quickly as possible. At the end of each run, five "booster" conditioning trials were used to minimize the extinction of fear responses to shock-paired stimuli. Stimuli are not drawn to scale.

Note that no electrical stimulation was administered during standard blocks (defined above). One to two shocks occurred in separate "filler" blocks, which had the same general structure as standard blocks, and were employed so as to avoid extinction. The responses of filler blocks were excluded from further data analysis.

The perceptual-decision phase was organized in eight separate "runs" (Figure 2C). Each run comprised six standard blocks and one filler block (in random order). Overall, for each participant and for each color condition, 48 trials were employed for each intensity level (twelve identities × four repetitions). After these blocks, to minimize extinction of fear responses to shock-paired faces, five "booster" conditioning trials were shown: one trial for each of the 4 trial types (two colors × two expressions), and one additional CS+ trial with shock (shock-paired, 100% fearful face). The schedule of stimulus presentation, triggering of shocks, and behavioral response acquisition were controlled by Presentation software (Neurobehavioral Systems, Albany, CA).

Control Session

To examine perceptual decisions made without the influence of the conditioning procedure, 12 participants (11 responders) participated in a control session 3–5 days after the first experimental session. The structure of the control session was identical to the main session, except that it did not involve conditioning. Participants were explicitly instructed that conditioning was not involved, and all conditioning-related equipment (e.g., shock stimulator) was removed from the testing room to minimize any contextual generalization effects. During the control session, faces were shown in both red and blue colors.

Psychometric Fits

Psychometric curves were fitted by using the Naka-Rushton contrast response model (Albrecht & Hamilton, 1982; Sclar, Maunsell, & Lennie, 1990). Curve fitting was performed with the MATLAB curve fitting toolbox (Mathworks, Natick, MA) and used a maximum likelihood criterion. The parameters $R_{\max}$, C_{50}, and M (see Equation 1) were constrained to vary from zero to one.

Results

To verify the effectiveness of the fear conditioning procedure, we contrasted SCRs evoked by CS+ faces (shock-paired, 100% fearful faces) and CS- faces (shock-paired neutral; unpaired neutral; unpaired fearful) during the conditioning phase. Note that, during conditioning, only 100% fearful faces were paired with shock, such that the conditioned stimuli involved a combination of *both* facial expression and color. We thus refer to "shock-paired" faces as those of the same color as the 100% fearful face that was paired with shock (the CS+ stimulus); faces shown in the other color are referred to as "unpaired" (see Figure 2B). We focused our analyses on 20 "responders," namely, participants whose SCRs evoked during CS+ trials (shock-paired 100% fearful, .28 ± .06 μS) were stronger than SCRs evoked during CS- trials (unpaired 100% fearful .02 ± .09 μS; shock-paired neutral .12 ± .05 μS; and unpaired neutral .02 ± .05 μS; all p's < .05). Thus, six participants were excluded from subsequent analyses because they did not exhibit reliable conditioning (larger responses to CS+ relative to CS-unpaired, 100% fearful faces).

Average data for the perceptual decision task are shown in Figure 3A. Participants reported "fearful" more often for shock-paired relative to unpaired conditions for the intermediate intensity levels of the graded faces. To examine the effect of affective learning on perceptual decisions, we employed a 2 × 11 (color: shock-paired, unpaired; intensity: 11 levels) repeated-measures ANOVA. The results revealed a significant color by intensity interaction [$F(10, 190) = 2.77$, $p < .01$, $\eta^2 = .13$], and main effects of color and intensity [$F(1, 19) = 13.93$, $p < .01$, $\eta^2 = .43$; $F(1, 10) = 494.28$, $p < .001$, $\eta^2 = .96$]. Subsequent, simple-effects analyses revealed that the percentages of "fearful" responses for shock-paired faces were higher than those for unpaired faces for the 40%, 50% and 60% intensity levels [$t(19) = 2.32$, $p < .05$; $t(19) = 2.59$, $p < .05$; $t(19) = 4.49$, $p < .001$, respectively; note that only the p value at 60% would survive a multiple-comparisons correction]; no significant differences were observed for low and high levels near the prototypical neutral/fearful expressions (Figure 3B).

The above results reveal that faces presented in the shock-paired color were reported as "fearful" more often relative to unpaired faces for intermediate intensity values. Visual inspection of the results suggests that the changes are similar to those expected by an increase in "contrast gain" (see Figure 1). Thus, to further characterize our results, average data for shock-paired and unpaired conditions were independently fit (Figure 3A, solid and dashed lines) according to the Naka-Rushton contrast response model (Albrecht & Hamilton, 1982; Sclar et al., 1990):

$$r = R_{max}\left(\frac{C^n}{C^n + C_{50}^n}\right) + M,$$

(Equation1, Naka-Rushton Response Function)

where r represents the percentage of "fearful" responses, C is the graded face intensity level ("contrast"), C_{50} is the intensity at which response is half-maximal (also called "threshold"), n is the exponent that determines the slope of the function, $R_{\max}$ is the asymptote of the response function, and M is the response at the lowest stimulus intensity. For average data, the parameter estimates were $C_{50} = .534$, $R_{\max} = .897$, $n = 5.409$, and $M = .069$ for unpaired faces (see Figure 2A, dashed line), and $C_{50} = .507$, $R_{\max} = .917$, $n = 4.756$, and $M = .074$ for shock-paired faces (see Figure 2A, solid line). These parameters suggest that the only difference in the fits concerned the threshold value (C_{50}). To more rigorously compare Naka-Rushton parameters at the group level, each individual's responses for shock-paired and unpaired conditions were independently fit, yielding parameters that subsequently were compared via paired t tests. These tests revealed a significant difference for the C_{50} parameter (mean difference = .032, SE = .011) [$t(19) = -2.853$, $p = .01$], but no significant differences for the remaining parameters (all ps > .05).

Control Session

The data obtained during the control session closely overlapped with the unpaired condition (see Figure 4). Performing psychometric fits with the 11 participants who participated in the control

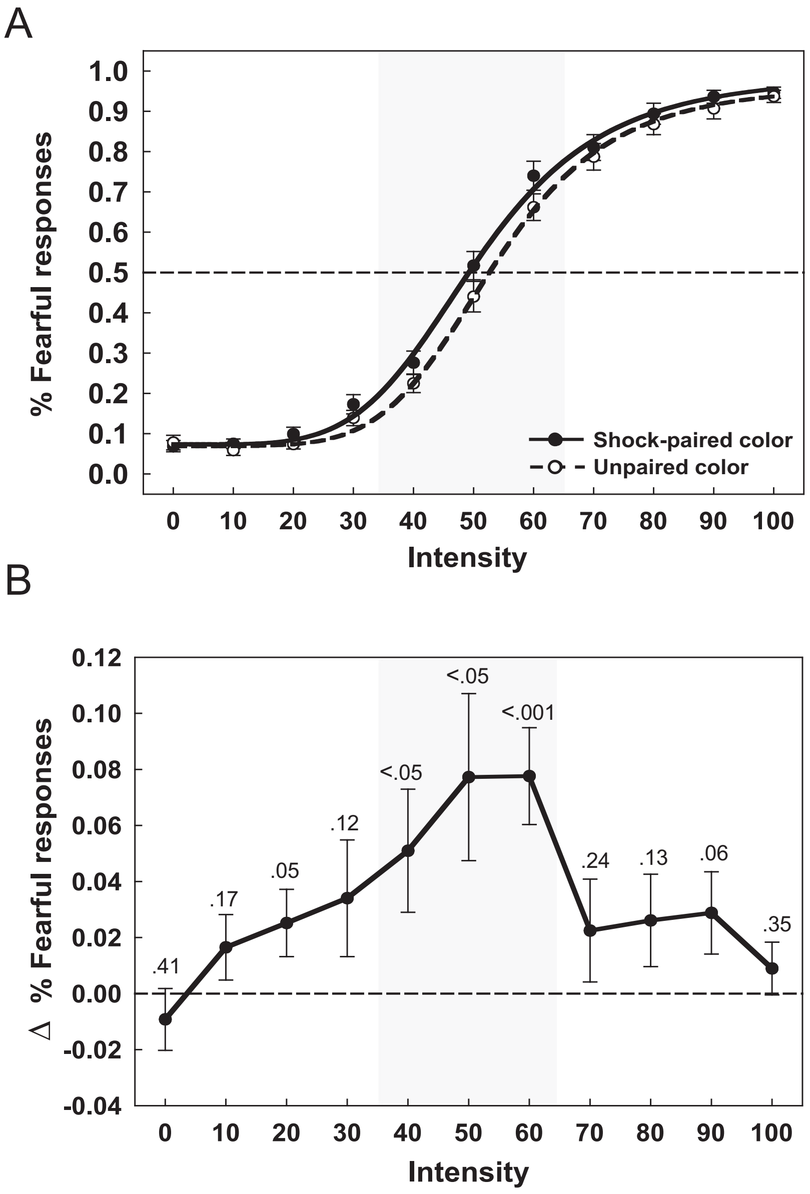

Figure 3. (A) Average percentage of "fearful" responses as a function of face intensity (from neutral to fearful, as shown in Figure 2A). Error bars indicate the standard error of the mean. The dashed line represents the psychometric fit to the unpaired condition and the solid line represents the psychometric fit to the shock-paired condition (both employed the Naka-Rushton response function). (B) Difference in the percentage of "fearful" responses in the shock-paired and the unpaired conditions. Positive values indicate higher frequencies for shock-paired relative to unpaired conditions. Error bars indicate the standard error of the mean. The values above error bars indicate statistical *p* values.

session and performing the corresponding paired *t* tests (see above), revealed significant differences in the threshold (C_{50}) between shock-paired and unpaired faces [$t(10) = -2.82$, $p < .05$], but no significant difference when comparing control faces and unpaired faces [$t(10) = .71$, $p = .50$].

Reaction Time Data

Finally, we investigated reaction times (RTs) during the perceptual decision task. Mean RTs were calculated for each face intensity level for both shock-paired and unpaired faces. Because the two-choice decision becomes more difficult around the point of subjective equality (PSE; i.e., the point at which participants report "fearful" 50% of the time), we expected RT to be slowest around the PSE and to be fastest at the extremes of the morphed faces (i.e., neutral and 100% fearful faces). Additionally, because fear detection occurs fast (Öhman, Flykt, & Esteves, 2001), we expected faster RTs for the prototypical fearful face relative to the prototypical neutral face. A 2 × 11 (color: shock-paired, unpaired;

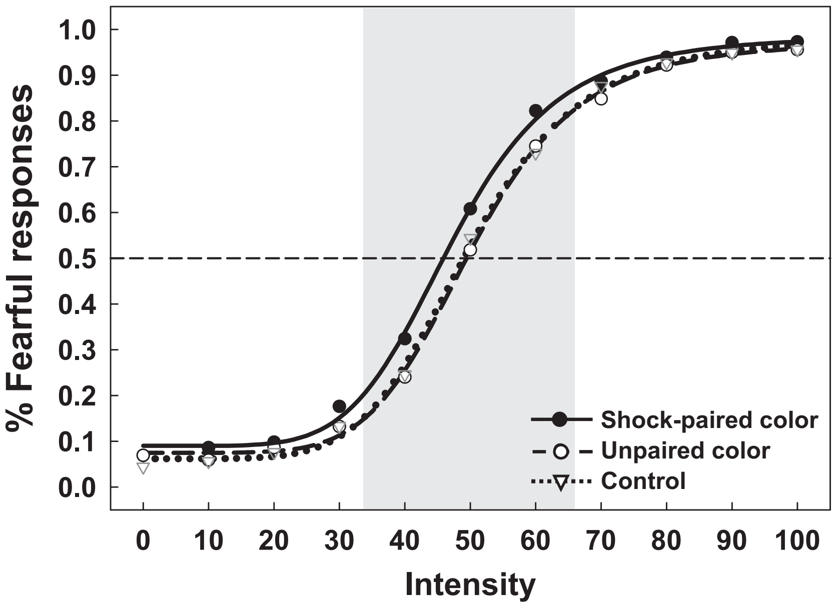

Figure 4. Average percentage of "fearful" responses as a function of face intensity for 11 participants who performed an additional control session. The dashed line represents the psychometric fit to the unpaired condition, the solid line represents the psychometric fit to the shock-paired condition, and the dotted line represents the psychometric fit to the control condition (all fits employed the Naka-Rushton response function). Error bars indicate the standard error of the mean.

intensity: 11 levels) repeated-measures ANOVA on RTs revealed a significant main effect of color [$F(1, 19) = 16.16, p < .01, \eta^2 = .46$], reflecting the fact that RTs to shock-paired faces (580.95 ± 19.68 ms) were faster than to unpaired faces (602.47 ± 22.26 ms) (see Figure 5). The main effect of intensity was also significant, as expected [$F(10, 190) = 14.79, p < .001, \eta^2 = .44$]. Consistent with our predictions, RTs exhibited both a significant quadratic trend [$F(1, 19) = 64.37, p < .001, \eta^2 = .77$] (reflecting an overall "inverted U" pattern), and a significant linear trend [$F(1, 19) = 7.24, p < .05, \eta^2 = .28$] (reflecting faster RT to higher relative to lower intensity faces). Finally, the interaction between color and intensity was significant [$F(10, 190) = 3.90, p < .001, \eta^2 = .17$]. Simple-effects analyses revealed significant RT differences for the intensity levels between 50% and 100% (all p's $< .05$; note that these values are not corrected for multiple comparisons), indicating that participants made quicker responses for shock-paired faces with intensities around the threshold level (C_{50}) – except for neutral faces (0%), for reasons that are not clear.

Discussion

How does the affective significance of an emotional face affect perceptual decisions? In the present study, we manipulated affective significance by pairing 100% fearful faces with aversive electrical stimulation. Our findings revealed that stimuli shown in the shock-paired color were more frequently reported as "fearful" relative to unpaired-color faces. Such increases in the frequency of "fearful" responses were most robust for faces at intermediate intensity levels (40–60% fearful). We further characterized the perceptual decisions under both conditions by performing psychometric fits to the data, which revealed significant increased sensitivity (i.e., leftward shift) for shock-paired relative to unpaired faces. Thus, despite identical physical features for shock-paired and unpaired stimuli (aside from the color, which was counterbalanced), more frequent "fearful" responses were made when participants viewed affectively significant stimuli. Finally, responses made to shock-paired stimuli were faster relative to unpaired faces for intensities in the range of 50% to 100%, supporting the idea

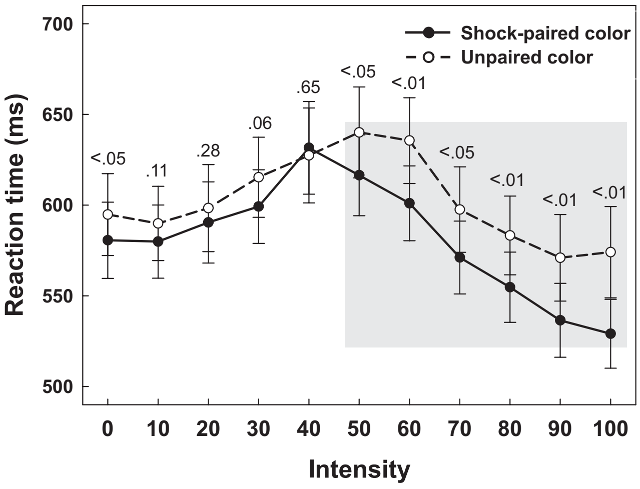

Figure 5. Mean reaction times during the perceptual decision task. Faster responses were observed for shock-paired faces relative to unpaired faces for graded faces of 50% intensity or higher (as well as neutral faces, 0%). Error bars indicate the standard error of the mean. The values above error bars indicate statistical p values.

that affective significance facilitated the speed of perceptual processing.

Previous research indicates that emotional expressions are perceived categorically (Calder, Young, Perrett, Etcoff, & Rowland, 1996; Etcoff & Magee, 1992). To investigate categorical perception, these studies employed graded stimuli (computer drawings, Etcoff & Magee, 1992; Ekman faces, Calder et al., 1996) while participants performed discrimination and identification tasks. These and other studies (e.g., (Campanella, Quinet, Bruyer, Crommelinck, & Guerit, 2002) suggest that small physical differences at emotion boundaries (e.g., sad-fear or happy-neutral) are perceived more accurately than equivalent differences between faces that are assigned the same emotion category (the signature for categorical perception). Although our study was not designed to investigate categorical perception, our results are largely consistent with previous findings. In particular, changes in the intensity of the stimulus for low-intensity stimuli (0–20%) and for high-intensity stimuli (70–100%) affected the decision to report "neutral" or "fearful" in only a minor way, if at all, whereas changes for intermediate-intensity stimuli (40–60%) had a significant effect (see below for RT differences). Given the leftward shift of the psychometric curve, our results also suggest that affective significance may be able to shift the categorical boundary between neutral and fearful faces. However, because our design was not aimed at determining potential category boundaries, further studies are needed to test this possibility.

The processing of emotional stimuli can have both advantageous and detrimental effects on behavioral performance in general and response time in particular. For instance, participants have been reported to be faster at detecting fearful or threatening target faces relative to neutral ones (Ishai et al., 2004; Öhman, Lundqvist, & Esteves, 2001) and facilitated search for discrepant fear-relevant pictures among fear-irrelevant pictures (Öhman, Flykt, & Esteves, 2001). At other times, RTs are slowed down when emotional stimuli are presented. For example, determining the orientation (upward/downward) of a target visual stimulus was shown to slow down following emotional pictures (Hartikainen, Ogawa, & Knight, 2000), and the presence of a central unpleasant picture was reported to increase RT when participants discriminated peripheral target letters (Tipples & Sharma, 2000) or the orientation of bars (Erthal et al., 2005). In both cases, the effects of emotional stimuli on performance have commonly been thought to be mediated by attention; (for discussion see Pereira et al., 2006). In the present study, participants reported "fearful" for stimuli shown in shock-paired color for stimuli in the range of 50% to 100% (in addition to 0% stimuli). Within this intensity range, average RT differences varied from 23 ms to 45 ms, revealing a considerable speed-up in RT for shock-paired stimuli. Of particular interest, the changes in RT were not confined to the intermediate intensity range that exhibited the largest changes in the percentage of "fearful" responses (40–60%) but clearly extended to less ambiguous faces, including 100% fearful faces. Thus, it appears that the speed-up occurred to faces that were closest to the CS+ (100% fearful), suggesting that 50–100% faces had increased affective significance to the participants. These results suggest some type of generalization gradient (Blough, 1975; Hull, 1943; Spence, 1937) such that the RT effects, which were maximal for 100% fearful faces, extended to other nonconditioned stimuli as a function of their similarity to the CS + stimulus.

What are the mechanisms by which affective significance modulated perceptual decisions? In the present experiment, affective significance was manipulated via fear conditioning, which is dependent on the amygdala in both nonhuman species and humans (Davis & Whalen, 2001; Phelps & LeDoux, 2005). In rats, such process critically depends on the central nucleus of the amygdala (LeDoux, Iwata, Cicchetti, & Reis, 1988), and amygdala lesions in humans eliminate fear conditioning (LaBar, LeDoux, Spencer, & Phelps, 1995). Given the involvement of the amygdala in fear conditioning, the source of the increased sensitivity observed here was, in all likelihood, related to this structure. In monkeys, the amygdala receives highly processed visual input from inferior temporal areas TEO and TE (Amaral, Behniea, & Kelly, 2003). At the same time, the amygdala projects to several levels of visual processing, including as early as V1, which allows it to influence visual processing according to the valence of the stimulus (Amaral et al., 2003). In our experiment, it is conceivable that prior learning (i.e., conditioning) affected cortical representations of faces in regions such as the fusiform gyrus (Haxby et al., 2001), much like changes reported in auditory cortex receptive fields following fear conditioning (Weinberger, 2004). In a recent study, Stolarova et al. (Stolarova, Keil, & Moratti, 2006) obtained evidence that early evoked responses in visual cortex (the C1 ERP component) were modulated by an item's prior history (pairing with aversive images). Because the C1 component occurred very early (65–90 ms post stimulus), they interpreted their results in terms of reorganization in visual cortex, which would enable sensory amplification of visual features that were related to motivationally relevant information. Alternatively, in our experiment, "feedback" signals from the amygdala at the time of stimulus presentation may have enhanced the representation of faces in visual cortex and have led to enhanced processing. In this context, Phelps et al. (2006) reported that fearful faces appear to enhance detection sensitivity in a way that is similar to the effects of attention. Specifically, a briefly flashed fearful face enhanced the detection sensitivity of subsequently presented gratings (Gabor patches). Finally, whereas the above two scenarios assume that fear conditioning may have modulated sensory processing per se, an alternative possibility is that conditioning affected processing at "later" stages, possibly those more directly linked to decision making. Thus, whereas affective significance increased the sensitivity to graded faces, further studies are required to elucidate the mechanisms by which shock-paired faces were linked to increased "fearful" responses in the present study.

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Received 03/22/2007
Revision received 10/23/2007
Accepted 10/25/2007 ■