

ORIGINAL ARTICLE

Here Comes Trouble: Prestimulus Brain Activity Predicts Enhanced Perception of Threat

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Abstract

Research on the perceptual prioritization of threatening stimuli has focused primarily on the physical characteristics and evolutionary salience of these stimuli. However, perceptual decision-making is strongly influenced by prestimulus factors such as goals, expectations, and prior knowledge. Using both event-related potentials and functional magnetic resonance imaging, we test the hypothesis that prior threat-related information and related increases in prestimulus brain activity play a key role in subsequent threat-related perceptual decision-making. After viewing threatening and neutral cues, participants detected perceptually degraded threatening and neutral faces presented at individually predetermined perceptual thresholds in a perceptual decision-making task. Compared with neutral cues, threat cues resulted in (1) improved perceptual sensitivity and faster detection of target stimuli; (2) increased late positive potential (LPP) and superior temporal sulcus (STS) activity, both of which are measures of emotional face processing; and (3) increased amygdala activity for subsequently presented threatening versus and neutral faces. Importantly, threat cue-related LPP and STS activity predicted subsequent improvement in the speed and precision of perceptual decisions specifically for threatening faces. Present findings establish the importance of top-down factors and prestimulus neural processing in understanding how the perceptual system prioritizes threatening information.

Key words: ERP, fMRI, LPP, perceptual decision-making, STS

Introduction

Emotional stimuli exist in a visually complex environment and making precise perceptual decisions about their presence is critical for survival. Perceptual prioritization of threatening stimuli has been attributed to the relatively automatic processing of these stimuli (Ohman et al. 2001). However, the transformation of sensory input into percepts is heavily influenced by “prestimulus” factors, including goals, expectations, and prior knowledge about the environmental context (Summerfield and de Lange 2014). Despite the importance of these prestimulus factors in perceptual decision-making, their role in facilitating threat perception remains unexamined. Does prior threat-related information enhance perception more than neutral information? Is the

facilitating effect of prior threat-related information implemented via changes in prestimulus neural activity?

Increases in prestimulus neural activity have been shown to bias subsequent perceptual decision-making. In monkeys, greater prestimulus activity is evident in neurons coding for expected stimuli (Sakai and Miyashita 1991; Schlack and Albright 2007; Albright 2012). In humans, cues predicting the occurrence of a face lead to increases in blood-oxygen-level-dependent (BOLD) signal in fusiform gyrus (Bar et al. 2001; Puri et al. 2009; Esterman and Yantis 2010). Prestimulus BOLD signals in extrastriate visual cortex predict whether Rubin’s vase illusion will be perceived as a face or a vase (Hesselmann, Kell, Eger, et al. 2008) and whether dots are perceived as moving randomly or coherently (Hesselmann, Kell and Kleinschmidt 2008). Increased prestimulus activity is linked

to improved perceptual performance (Super et al. 2003; Boly et al. 2007; Scholvinck et al. 2012), and may reflect increased prestimulus attention, thereby improving subsequent detection (Hesselmann et al. 2010). Alternatively, according to sequential sampling models of perceptual decision-making (Ratcliff 1978; Ratcliff and Smith 2004), increased prestimulus activity may reflect a shift in the starting point for the accumulation of evidence toward a specific decision boundary (Summerfield and de Lange 2014).

Overall, these findings suggest that prior information regarding threat and associated prestimulus neural changes may be a key factor in enhancing threat-related perceptual decision-making. In 2 studies, we examined this hypothesis using a perceptual decision-making task in which participants were cued to detect fearful or neutral faces, degraded to their predetermined perceptual threshold, while signal detection, event-related potential (ERP) and functional magnetic resonance imaging (fMRI) measures were recorded. We manipulated the threatening nature of the cue by asking participants to respond if they saw a fearful face or not on fear cue trials, or if they saw neutral face or not on neutral cue trials. Cues did not indicate the likelihood of upcoming facial stimuli. Hence, the task design encouraged participants to use 2 perceptual “sets,” one to detect fearful and another to detect neutral perceptually degraded faces (Dayan et al. 1995; Doshier and Lu 1999; Summerfield et al. 2006; Casale and Ashby 2008; Summerfield and Koechlin 2008; Summerfield and Egner 2009; Kok et al. 2012; Wyart et al. 2012).

To investigate whether cue-related prestimulus neural activity enhances perception of threatening stimuli, in the ERP study we examined the cue-related late positive potential (LPP), an ERP component associated with enhanced perceptual processing of emotional stimuli (Schupp et al. 2000; Weinberg et al. 2012). Additionally, we examined face stimulus-related LPP (Schupp et al. 2004) as well as vertex-positive potential (VPP/N170), because VPP is involved in processing the structural aspects of faces (Jeffreys 1996) and is also impacted by emotional face perception (Williams et al. 2006). In the ERP study, we tested 3 hypotheses: (1) Perceptual decisions regarding fearful faces will be facilitated by fear versus neutral cues, (2) The LPP will be greater for fearful versus neutral faces and cues, indicating that this neural index of emotional face processing is also sensitive to upcoming perceptual decisions regarding fearful faces, and (3) Fear cue-elicited LPP will predict improved behavioral performance, indicating that changes in prestimulus neural activity aid in subsequent threat-related perceptual decisions.

Similarly, in the fMRI study, we separately examined cue- and stimulus-related BOLD signal in the superior temporal sulcus (STS) and the amygdala, brain regions that are critical for perception of emotional faces (Hasselmo et al. 1989; Ojemann et al. 1992; Adolphs 2002; Vuilleumier 2005; Engell and Haxby 2007; Said et al. 2011). STS has been shown to be more active for emotionally expressive compared with neutral faces (Engell and Haxby 2007), and representations of emotional expressions in STS have been decoded using fMRI (Said et al. 2010). The amygdala is also more active in response to emotional faces and lesions in the amygdala lead to deficits in emotional face perception (Adolphs 2002; Vuilleumier 2005). In addition, we examined cue- and stimulus-related activity in the fusiform face area (FFA), a brain region that is involved in processing invariant aspects of faces such as identity (Haxby et al. 2000). While LPP offers high temporal resolution, it may reflect a composite of activity from extrastriate occipital and inferior temporal cortices (Sabatinelli et al. 2007). Using fMRI allowed us to focus on neural activity in areas that are sensitive specifically to emotional face processing to determine whether these regions are also activated for cues that

indicate forthcoming threatening perceptual decisions. In the fMRI study, we predicted that: (1) Perceptual decisions regarding fearful faces will be facilitated by fear versus neutral cues, (2) Activity in STS and the amygdala will be greater for fearful versus neutral faces and cues, indicating that activity in this region is sensitive not only to threatening face processing but also to upcoming perceptual decisions regarding threatening faces, and (3) Fear cue-elicited brain activity will predict improved behavioral performance, indicating that prestimulus increases in a brain region sensitive to emotional expressions aids in subsequent threat-related perceptual decisions.

Materials and Methods

Participants

Twenty-two students from Stony Brook University participated in the ERP study and 18 students participated in the fMRI study for class credit or payment. All participants gave informed consent and the study was approved by the Stony Brook University Institutional Review Board. Participants reported no history of neurological or psychiatric illness or fMRI contraindications. For the ERP study, 1 participant was excluded from the behavioral analyses due to poor behavioral performance, and 2 additional participants were excluded from the ERP analyses due to poor quality electroencephalography (EEG) recordings, resulting in a sample of 21 participants (14 women; mean age 20.60 ± 1.08 years) for the behavioral analyses and 19 participants (12 women; mean age 20.40 ± 0.97 years) for ERP analyses. For the fMRI study, 1 participant refused to continue the experiment due to discomfort in the magnet. Therefore, a sample of 17 (12 women; mean age 25.8 ± 3.21 years) participants was used in the behavioral analyses. Additionally, the fMRI data for 2 subjects was not usable due to technical problems, resulting in 15 participants (10 women; mean age 25.73 ± 3.35 years) for fMRI analyses.

Experimental Paradigm

Stimuli

Sixteen fearful male faces (FF) and neutral male faces (NF) from the Nim Stim set (Tottenham et al. 2009) were modified from color to grayscale (512×512 pixels) and equalized for luminance and spatial frequency using the SHINE (Spectrum, Histogram, and Intensity Normalization and Equalization) toolbox for Matlab (Willenbockel et al. 2010). This toolbox has been used effectively to minimize confounds due to low-level image properties in studies examining top-down processes such as goals and expectations in face perception (Fiset et al. 2008). While both fearful and angry faces are considered threat signals, we chose to use fearful faces only, because, compared with angry faces, fearful faces have been shown to be more threatening (Taylor and Barton 2015) and to lead to greater activation of threat-related neural circuits (Whalen et al. 2001). Angry faces are also thought to evoke a more complex response requiring the observer to respond directly to the interaction (Pichon et al. 2009), which suggests that fearful faces provide responses more clearly linked to threat alone. Perceptual masks made from face stimuli, possessing the same low-level image properties, followed each stimulus. The same stimuli were used in the ERP and the fMRI study.

Threshold Task

For both the ERP and fMRI studies, each participant's threshold for perception (75% correct) was determined separately for FF and NF images using a perceptual discrimination task

(Summerfield et al. 2006). Images were presented in 16 blocks of 16 trials each, resulting in 128 FF trials and 128 NF trials using Psychopy software (Peirce 2007). On each trial, a fixation cross (2–3 s in the ERP study; 3–7 s in the fMRI study) was followed by a perceptually degraded FF or NF image (100 ms), which was followed by a mask (300 ms). Participants identified the face as fearful or neutral by pressing one of 2 adjacent buttons on a keyboard (Fig. 1A). Contrast was manipulated on a scale ranging from 1 to 0, such that 1 corresponded to no contrast manipulation and 0 corresponded complete removal of contrast from the image, leaving it as a gray square. FF and NF images were initially presented at a reduced level contrast at 0.1, making images visible, but not easy to see. Stimulus contrast on subsequent trials was governed by 2 adaptive staircases (Watson and Pelli 1983), which allowed inferences about the subjective perceptual thresholds for that participant (Fig. 1B). Thresholds were measured and adjusted using a Weibull psychometric function such that an incorrect answer led to an easier-to-see stimulus (image presented at a higher contrast level) on the next trial, while a correct answer led to a more perceptually challenging stimulus presentation (lower contrast) on the next trial (Watson and Pelli 1983).

Cued Discrimination Task

In a subsequent task, used in both the ERP and fMRI studies (Fig. 1D), subjects viewed the FF and NF images from the thresholding task in the same manner but with 4 main differences. First, FF and NF were perceptually degraded and presented at one of 8 contrast levels ranging from 6% less to 8% more than the participant's previously determined perceptual threshold. For example, if a participant's threshold for fearful faces was determined to be 0.1, they were subsequently shown images ranging from 0.108 to 0.094. Stimuli were shown at several contrast levels to prevent improved perceptual performance due to practice effects (Adini et al. 2004). Second, prior to each FF or NF, the letter "F" (fearful cue; FC) or "N" (neutral cue; NC) appeared for 1 s. The cue was not indicative of the probability of an upcoming stimulus type: an equal number of FF and NF trials were presented after each cue type. Third, on FC trials, participants responded by pressing the "yes" button if the stimulus

was a FF, and the "no" button if it was not. Similarly, on NC trials, participants pressed the "yes" button if the stimulus was a NF, and the "no" button if it was not (Fig. 1C). Participants responded with 2 fingers using 2 adjacent keyboard buttons.

Finally, the timelines of the tasks were different depending on whether EEG or fMRI data were being acquired. The timing parameters of the EEG task were identical to those of the thresholding task: fixation (2–3 s jittered), cue (1 s), jittered delay (2–3 s), and stimulus (100 ms). However, the timing parameters in the fMRI study were optimized to enable us to statistically dissociate BOLD responses related to cue processing from those related to stimulus processing. To do so, the interval duration between cue (1 s) and stimulus (100 ms) was jittered, ranging from 3 to 7 s (in 1 s bins), along a pseudoexponential distribution of 3 s (50%), 4 s (25%), 5 s (12%), 6 s (6%), and 7 s (6%) intervals (Ollinger, Corbetta, et al. 2001; Ollinger, Shulman, et al. 2001; Wager and Nichols 2003). To further decorrelate cue from stimulus processing, 20% of the trials were "catch trials," on which the cues were not followed by a stimulus (Ollinger, Corbetta, et al. 2001). During data analysis, variance accounted for by the cue versus stimulus period was modeled by separate regressors to examine their respective contributions. To dissociate stimulus-related activity from subsequent cue-related activity, the inter-trial interval duration was varied in the same way as the cue-stimulus interval duration. Evidence from both computational modeling and empirical research suggest that the temporal jittering proposed for the current study ensures a reliable distinction of BOLD signal attributable to successive events (Dale 1999; Corbetta et al. 2000; Ollinger, Corbetta, et al. 2001; Ollinger, Shulman, et al. 2001; Wager and Nichols 2003). Reaction time and accuracy data were recorded allowing us to compute measures of hit rate, false alarm rate, perceptual sensitivity (d'), and bias (c).

Control Experiment

To confirm that the effect of FC is specific to the threatening nature of the cues as opposed their general salience, we conducted a behavioral pilot study in which participants were asked to respond to happy (HF) and neutral (NF) faces preceded by happy (HC) and neutral (NC) cues. HF are considered salient

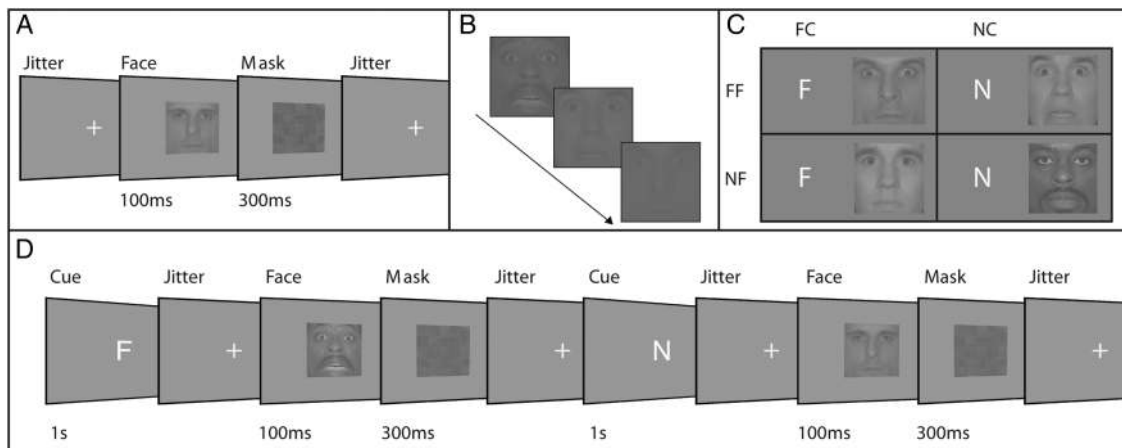


Figure 1. (A) Threshold task timeline. Participants performed a 2-alternative forced-choice discrimination task on degraded fearful and neutral faces to determine perceptual thresholds (75% correct) for each stimulus type. The duration of the fixation cross presentation was jittered, and varied between 2 and 3 s in the ERP study and between 3 and 7 s in the fMRI study. (B) Adaptive staircases, which made images harder or easier to see based on subject responses, were used in the thresholding task to find each participant's perceptual threshold for fearful and neutral faces. (C) Cue and stimulus combinations in the cued discrimination task: fearful cue/fearful face (FC/FF), neutral cue/fearful face (NC/FF), fearful cue/neutral face (FC/NF), and neutral cue/neutral face (NC/NF). (D) Cued discrimination task timeline. Participants viewed the same fearful and neutral faces, but the images were preceded by "F" or "N" cues which indicated whether the upcoming decision was "fearful face or not" or "neutral face or not." The duration of the fixation cross presentation was jittered, and varied between 2 and 3 s in the ERP study and between 3 and 7 s in the fMRI study.

like FF; however, unlike negatively valenced FF, HF are positively valenced stimuli (Murphy and Zajonc 1993). The threshold and cue tasks employed in this experiment were identical to ones described above, except HF were presented instead of FF. Twenty-three Stony Brook students (18 women; mean age 20.09 ± 1.47 years) gave informed consent and completed the tasks. The study was approved by the Stony Brook University Institutional Review Board. Data from 1 participant was excluded due to technical problems, for a final sample of size of 22 (17 women; mean age 20.14 ± 1.50 years).

EEG Data Acquisition and Preprocessing

Continuous EEG recordings were collected from 34 electrodes, as well as the right and left mastoids using the ActiveTwo BioSemi system (BioSemi, Amsterdam, the Netherlands: <http://www.biosemi.com>). Electrooculogram generated from eye movements and eyeblinks was recorded using 4 facial electrodes. The EEG signal was preamplified at the electrode and digitized at a sampling rate of 512 Hz, using a low-pass fifth order sinc filter with -3 dB-cutoff point at 104 Hz. Each active electrode was measured online with respect to a common mode sense active electrode. Offline, all data were referenced to the average of the mastoids, and band-pass filtered with low and high cutoffs of 0.01 and 30 Hz, respectively; eye blink and ocular corrections were conducted as described by Gratton et al. (1983).

A semiautomatic procedure was employed for artifact rejection. The criteria applied were a voltage step of more than $50.0 \mu\text{V}$ between sample points, a voltage difference of $300.0 \mu\text{V}$ within a trial, and a maximum voltage difference of $<0.50 \mu\text{V}$ within 100 ms intervals. Visual inspection of the data was then conducted to detect and reject any remaining artifacts.

EEG Data Analysis

The EEG collected during the cueing task was segmented for each trial beginning 200 ms before the onset of either the cue or the face and continuing for 1200 ms (i.e., for 1000 ms following the presentation of the cue or the face); a 200 ms window prior to stimulus onset served as the baseline. ERPs were constructed by separately averaging for each cue type (FC, NC) and face type (FF, NF). The LPP is maximal at centro-parietal sites; because there is evidence that early and late time-windows of the LPP may be functionally distinct, the LPP was scored at Pz in 2 separate time-windows (Olofsson et al. 2008; Foti et al. 2009) as the average activity between 300 and 600 ms and between 600 and 1000 ms. We also examined the face-elicited vertex positive potential (VPP/N170), an ERP measure that reflects structural aspects of face processing (Jeffreys 1996). The VPP and the N170 are the same ERP: the VPP is evident when using a mastoid reference, the N170 is evident when using an average reference (Joyce and Rossion 2005). The VPP is typically maximal at central sites when using the mastoid reference; it was therefore scored as the average activity between 200 and 300 ms at the average of Cz and FCz.

In addition, we investigated whether neural response to the cues facilitated subsequent perception of faces; Pearson's correlations were used to correlate cue-elicited LPPs with behavioral measures of perception including d' , accuracy, and reaction time (RT) across subjects. Previous studies have shown that prestimulus cuing and related neural activity is associated with better perception of the cued compared with uncued stimulus (Summerfield et al. 2006; Kentridge et al. 2008; Summerfield and Koehlin 2008; Kok et al. 2012). Therefore, we hypothesized

that (1) greater FC-elicited LPP would be associated with improved perception of FF compared with NF, and (2) greater FC-elicited versus NC-elicited LPP would be associated with improved perception of subsequently presented FF. These specific predictions were tested by comparing the correlations with one-tailed Pearson-Filon tests (Diedenhofen and Musch 2015). Furthermore, to investigate whether cue-related LPP predicts behavior not only between subjects but also within subjects, we examined whether cue-elicited LPP differed for fast versus slow trials. Median RTs to the faces were calculated for each cue-face combination separately for each individual subject. Grand average ERPs for each subject were then constructed by separately averaging ERPs to the cue that preceded correct trials with RTs to faces falling below that individual's median score (i.e., fast RTs) and above each individual's median score (i.e., slow RTs). Thus, 8 new cue-locked ERP averages were created for each subject: FC/FF fast, FC/FF slow, FC/NF fast, FC/NF slow, NC/FF fast, NC/FF slow, NC/NF fast, and NC/NF slow. The LPP to the cue was scored as above. Because 2 subjects had too few trials falling below their median RT in several of the eight averages, reliable LPPs could not be scored (Moran et al. 2013). These analyses are therefore based on 17 subjects.

fMRI Data Acquisition and Preprocessing

Structural and BOLD data were acquired on a 3 T Siemens Trio-Tim whole-body scanner. Functional volumes were acquired with an interleaved echoplanar imaging sequence using the following parameters: 2300 ms repetition time (TR), 30 ms echo time (TE), 33 axial slices, slice thickness: 3 mm, in-plane resolution: 1.72×1.72 , field of view (FOV): 220 mm flip angle 90° . Structural images were acquired via sagittal magnetization prepared rapid gradient echo (MPRAGE) sequence (TR = 1900 ms, TE = 2.53 ms, flip angle = 9° , slice thickness = 1 mm, in-plane resolution = 1×1 mm).

Functional images for each participant were corrected for slice timing, spatially realigned, spatially normalized using the Montreal Neurological Institute (MNI) template brain, and smoothed with an isotropic Gaussian kernel of full-width half-maximum (FWHM) of 6 mm^3 using Statistical Parametric Mapping (SPM8; Wellcome Department of Cognitive Neurology, London, UK). The ARTRepair toolbox (<http://cibsr.stanford.edu/tools/ArtRepair/ArtRepair.htm>) was used to correct motion artifact by replacing affected volumes with a volume interpolated from the nearest unaffected volumes.

fMRI Data Analyses

Cued Discrimination Task Analyses

For each subject, BOLD contrast data were modeled separately for each cue type (FC and NC) and stimulus type (FF and NF) for each session using stick (delta) functions convolved with the canonical hemodynamic response function in a general linear model (GLM). The GLM also included a 128 s high-pass filter to remove low-frequency fluctuations and an autoregression (1) model to account for temporal nonsphericity due to autocorrelations. Model estimation in SPM resulted in 6 parameter estimates (β) per session, 2 that modeled cue-related activity for FC and NC and 4 that modeled stimulus-related activity for cue/stimulus pairs FC/FF, FC/NF, NC/FF, and NC/NF for each and every voxel. Contrast maps corresponding to each cue and stimulus type were created using β s across sessions. To examine group-level differences in cue-related activity, the contrast maps corresponding to FC and NC were compared using a voxelwise paired sample

t-test across subjects. To examine differences in stimulus-related activity, stimulus-related contrasts were entered into a mixed-model analysis of variance (ANOVA) in SPM8 with subjects as a random factor and cues (FC and NC) and stimulus (FF and NF) as fixed factors.

To examine whether increases in neural responses to FC facilitated subsequent perceptual decisions about faces, we conducted voxelwise multiple regression analyses with prestimulus activity in our anatomical regions of interest (ROIs) predicting improvements in *d'*, accuracy, and RT for detection of subsequently presented faces, across subjects. Given that prestimulus cuing and related neural activity is associated with better perception of the cued compared with uncued stimulus (Adolphs 2002; Summerfield et al. 2006; Kentridge et al. 2008), we proposed that (1) greater FC-elicited brain activity in our ROIs will be associated with improved FF compared with NF perception and (2) greater FC versus NC-elicited brain activity will be associated with improved perception of subsequently presented FF. These specific predictions were tested by comparing the correlations with one-tailed Steiger's *Z* test (Steiger 1980) and conducting regression with FC and NC cue-related activity predicting subsequent FF accuracy.

In addition to examining the relationship between prestimulus brain activity and subsequent behavior across subjects, we also examined this relationship within subjects. We did this by estimating another model in SPM8 that was similar to the one described above, but also included condition-specific regressors that modeled RT as a continuous factor (referred to as parametric modulation in SPM8). These regressors allowed us to identify voxels in which brain activity was significantly correlated with subsequent RT on a trial-by-trial basis. We then examined the relationship between prestimulus activity and behavior in our ROIs described below.

Since our hypotheses focus on how cues enhance perceptual decisions regarding threatening faces, we focused on the STS and the amygdala, regions that are known to be important in emotional face processing (Hasselmo et al. 1989; Sugase et al. 1999; Haxby et al. 2000; Adolphs 2002). To ensure independence between the ROI selection process and subsequent testing of contrasts between experimental conditions, STS ROIs were defined bilaterally as 10 mm spheres centered around activation peaks in STS ($\pm 48, -58, 12$) identified in a large scale, factorial study of face perception as peak voxels more sensitive to faces (Rossion et al. 2012). Amygdala ROIs were defined using automated anatomical parcellation in SPM (Tzourio-Mazoyer et al. 2002). A corrected significance level of $P < 0.05$ was achieved for bilateral STS and amygdala ROI analyses via Monte Carlo simulations implemented in AlphaSim toolbox (AFNI; http://afni.nimh.nih.gov/pub/dist/doc/program_help/AlphaSim.html). While STS is involved in the neural representation of facial expressions, FFA is important in processing of invariant aspects of faces, such as identity (Haxby et al. 2000). However, because some studies show that FFA is also sensitive to emotional content of faces (Adolphs 2002; Vuilleumier 2005), we conducted exploratory analyses at a reduced whole brain threshold of $P < 0.005$, uncorrected to investigate cue and stimulus-related changes in activity in this area.

Results

ERP Study

Behavioral

First, we examined the hypothesis that the prior threat-related information will increase the sensitivity and speed of subsequent

perceptual decisions. FC resulted in greater *d'* ($M = 2.88 \pm 0.67$) than NC ($M = 2.06 \pm 0.88$), $t_{20} = 4.50$, $P = 2.21 \times 10^{-4}$, $d = 2.01$, indicating that for the same set of faces, FC facilitates threat-related perceptual decisions more than NC facilitates neutral perceptual decisions (Fig. 2A). To determine what drives this difference in *d'*, we examined the contributions of hit rate and false alarm rate. The cue-related facilitation of perceptual sensitivity was affected by stimulus type, with greater hit rate for FC trials (correctly identifying FF $M = 0.90 \pm 0.07$) compared with NC (correctly identifying NF; $M = 0.79 \pm 0.14$; $t_{20} = 3.85$, $P = 0.001$, $d = 1.72$), but no difference in false alarm rate (M for FC = 0.10 ± 0.08 ; M for NC = 0.15 ± 0.11 ; $t_{20} = -1.92$, $P = 0.07$, $d = 0.86$; Fig. 2B). To compare the impact of FC and NC on subsequent FF perception, we also compared the hit rate for FC trials to the correct rejection rate for NC trials ($M = 0.85 \pm 0.11$), and found that the FC led to greater subsequent accuracy of FF detection ($t_{20} = 3.65$, $P = 0.002$, $d = 1.63$). Next we examined response bias (*c*). However, we found no difference in bias on FC ($M = 0.02 \pm 0.33$) versus NC trials ($M = 0.08 \pm 0.21$).

Reaction time results in Figure 2C showed main effects of cue type ($F_{1,20} = 105.67$, $P = 1.98 \times 10^{-9}$, $\eta p^2 = 0.84$), such that FC resulted in faster identification of subsequent stimuli than NC. Additionally, there was a main effect of stimulus type ($F_{1,20} = 20.10$, $P = 2.28 \times 10^{-4}$, $\eta p^2 = 0.50$), and interaction of cue type and stimulus type ($F_{1,20} = 22.53$, $P = 1.23 \times 10^{-4}$, $\eta p^2 = 0.53$) such that FC resulted in faster identification of FF ($M = 1.05 \pm 0.14$) than NF ($M = 1.19 \pm 0.15$), mean difference = -0.14 $P = 4.89 \times 10^{-6}$ but the same difference was not seen for NC's impact on FF ($M = 1.22 \pm 0.14$) and NF RT ($M = 1.24 \pm 0.13$). Hence, RT results provide support for the differential impact of FC and NC on subsequent perception, with only FC speeding perceptual decision-making for FF but not NF. Finally, present results were not due to differences in individual participant thresholds for fearful versus neutral faces on the threshold task ($t_{20} = -1.20$, $P = 0.24$, $d = 0.54$).

Control Experiment

To determine whether the perceptual enhancement seen due to threatening cues is seen for other salient cues, we compared the perceptual sensitivity for HC versus NC. We found no difference in perceptual sensitivity (*d'*) following HC ($M = 2.56 \pm 1.14$) compared with NC ($M = 2.34 \pm 0.64$), indicating that participants' ability to accurately discriminate between HF and NF was not improved by a preceding HC. This result stands in contrast with findings of improved perceptual sensitivity following FC, indicating that FC has a unique impact on subsequent perceptual sensitivity.

We also examined the impact of HC and NC on subsequent RT, using a 2 (cue type) \times 2 (stimulus type) repeated-measures ANOVA. We found a main effect of cue type ($F_{1,21} = 48.12$, $P = 7.48 \times 10^{-7}$, $\eta p^2 = 0.70$), such that HC was associated with faster RT than NC. There was also an interaction between cue type and stimulus type ($F_{1,21} = 22.46$, $P = 1.11 \times 10^{-4}$, $\eta p^2 = 0.52$), such that HC led to faster identification of HF compared with NF ($M = 1.01 \pm 0.04$), mean difference = -0.10 , $P = 0.006$, while NC led to faster identification of NF ($M = 1.15 \pm 0.03$) than HF ($M = 1.22 \pm 0.04$), mean difference = -0.07 , $P = 0.018$. Overall, our results show that salient HC improve RT like FC, but without the benefits in perceptual sensitivity seen due to FC.

ERP Results

First, we examined the prediction that the LPP would be greater for FC versus NC suggesting a mechanism by which prestimulus FC could perceptually prioritize FF perception. Consistent with

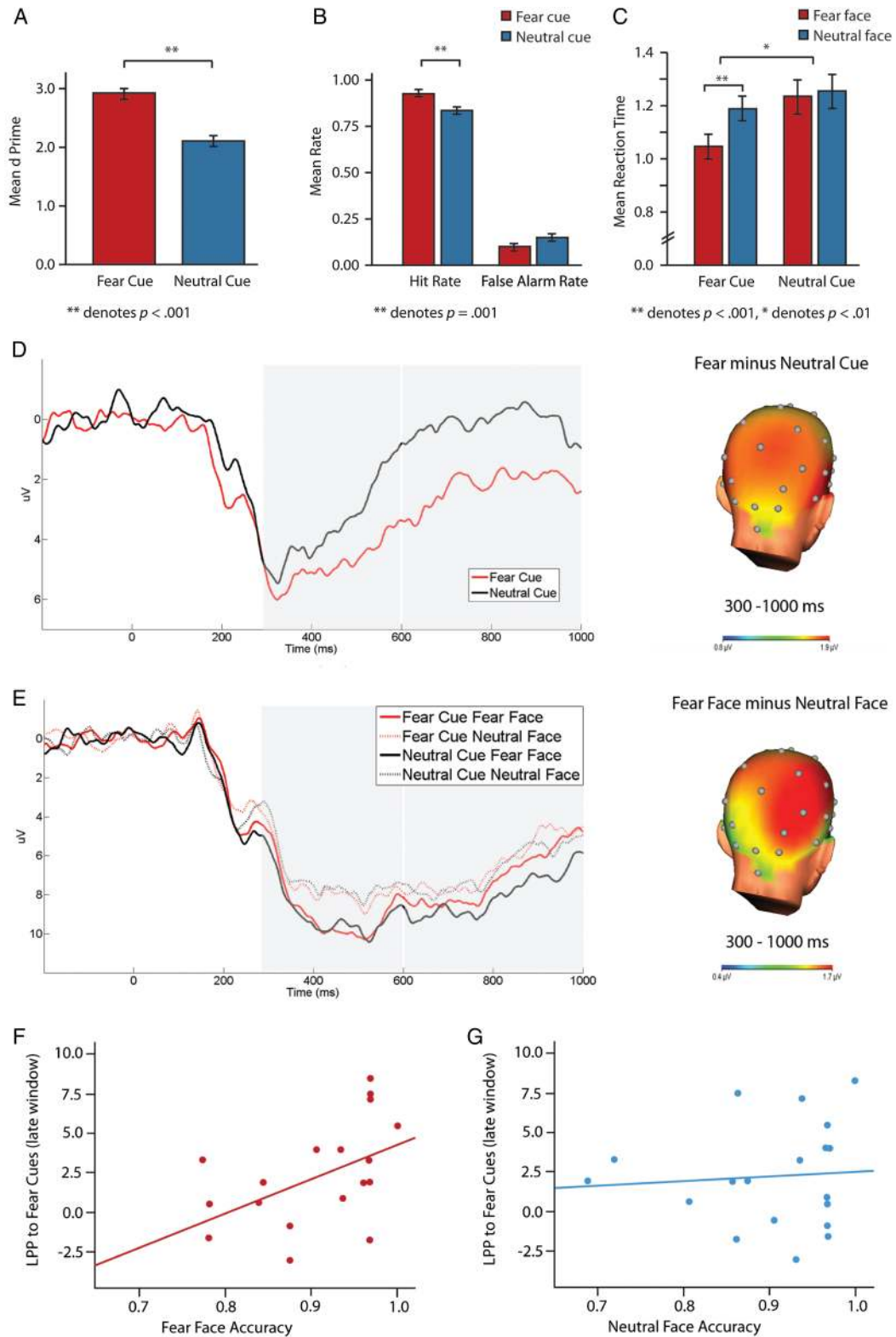


Figure 2. (A) Perceptual sensitivity (d'), for fear and neutral cue trials in the ERP study. Fear cues enhanced the sensitivity of perceptual decision-making more than neutral cues. (B) Hit and false alarm rates for fear and neutral cue trials. Fear cues resulted in higher hit rate for fearful faces than neutral cues for neutral faces. There was no difference for false alarm rates for fear versus neutral cues. (C) Reaction time for all cue/stimulus combinations. Fear cues lead to faster perceptual decision-making than neutral cues. Additionally, fear cues resulted in faster identification of fearful than neutral faces, but the same difference was not seen for neutral cues. (D) Topographic maps depicting voltage differences (in μ V) for fear minus neutral cues. Grand average stimulus-locked ERPs for each cue type show a larger LPP to fear (black) compared with neutral cues (gray). (E) Topographic maps depicting voltage differences (in μ V) for fearful minus neutral faces. Fearful faces were associated with a larger LPP compared with neutral faces (regardless of preceding cue type). (F) Greater LPP for fear cues is associated with greater accuracy for subsequent fear faces. (G) Greater LPP for fear cues was not associated with greater accuracy for neutral faces.

our prediction, FC elicited a larger LPP than NC, in the late time window (early window: $F_{1,18} = 4.19$, $P = 0.056$, $\eta^2 = 0.19$; late window: $F_{1,18} = 6.93$, $P = 0.02$, $\eta^2 = 0.28$; Fig. 2D). Next, emotional encoding of faces was examined by conducting a 2 (cue type) \times 2 (stimulus type) repeated-measures ANOVAs on the LPP elicited by threatening and neutral faces. FF elicited a larger LPP than NF, regardless of the preceding cue, in the early and the late time-windows (early window: $F_{1,18} = 6.92$, $P = 0.02$; $\eta^2 = 0.28$; late window: $F_{1,18} = 4.35$, $P = 0.05$; $\eta^2 = 0.20$; Fig. 2E).

Since some studies show VPP is also impacted by emotional face perception (Williams et al. 2006), ERP response to face stimuli in the time-window of the VPP was explored using a 2 (cue type) \times 2 (stimulus type) repeated-measures ANOVA. The effect of face type ($F_{1,18} = 3.85$, $P = 0.07$; $\eta^2 = 0.18$), cue type, ($F_{1,18} = 4.02$, $P = 0.06$; $\eta^2 = 0.18$), and the interaction between cue type and stimulus type did not reach significance, ($F_{1,18} = 2.59$, $P = 0.13$; $\eta^2 = 0.13$). This pattern of results is consistent with research demonstrating that the VPP better represents structural rather than emotional encoding of faces (Streit et al. 2000; Herrmann et al. 2002).

Relationship Between Cue-related ERP and Behavioral Performance

We examined the hypothesis that the magnitude of the LPP elicited by FC would predict behavior using Pearson's correlations between neural processing of the cues and perceptual sensitivity and accuracy in response to faces. Increased FC-elicited LPP activity was related to greater d' in the late time-window (early window: $r_{17} = 0.31$, $P = 0.20$; late window $r_{17} = 0.47$, $P = 0.04$), while NC-related LPP was not associated with d' (early window: $r_{17} = 0.28$, $P = 0.24$; late window $r_{17} = 0.11$, $P = 0.67$).

To determine whether there was a specific effect of FC-elicited LPP on FF detection, we first examined correlations between FC-elicited LPP and accurate identification of FF and NF. A significant relationship between FC-elicited LPP and FF accuracy was found in the late time-window (early window: $r_{17} = 0.41$, $P = 0.08$; late window: $r_{17} = 0.48$, $P = 0.04$) but no significant relationship was found between FC-elicited LPP and accurate identification of NF (early window: $r_{17} = -0.09$, $P = 0.72$; late window: $r_{17} = 0.08$, $P = 0.73$; Fig. 2F). Next, we tested the hypothesis that FC-elicited LPP predicts accurate detection of subsequently presented FF more than NF. We found FC-elicited LPP correlates more strongly with accurate detection of FF than accurate detection of NF (early window: $z = 1.80$, $P = 0.04$; late window: $z = 1.46$, $P = 0.07$). Furthermore, NC-elicited LPP activity was not related to the correct identification of subsequently presented FF, (early window: $r_{17} = 0.11$, $P = 0.66$; late window: $r_{17} = 0.01$, $P = 0.96$). Finally, FC-elicited LPP correlates more strongly with subsequent FF accuracy than NC-elicited LPP correlates with accurate detection of FF (early window: $z = 1.44$, $P = 0.08$; late window: $z = 2.00$, $P = 0.02$), supporting the idea that FC bears a unique relationship with enhanced perception of subsequently presented threatening stimuli.

Additionally, we examined whether cue-related LPP predicts behavior not only between subjects but also within subjects. For each subject we examined whether trials with enhanced cue-related LPP were associated with subsequent behavioral facilitation or interference by computing a 2 (cue type) \times 2 (stimulus type) \times 2 (RT: fast versus slow responses for that subject) repeated-measures ANOVA. A significant cue type by stimulus type by RT interaction in the early window ($F_{1,16} = 4.31$, $P = 0.05$; $\eta^2 = 0.21$) was further decomposed to a 2 (congruent versus incongruent cue-face pairings) \times 2 (response time) repeated-measures ANOVA and showed a significant speed by congruency interaction ($F_{1,16} = 4.31$, $P = 0.05$; $\eta^2 = 0.21$), such that on congruent trials, a larger LPP to the cue predicted faster responses to the stimuli (Cohen's $d = 0.53$), while on incongruent trials, a larger

LPP to the cue was instead associated with "slower" responses to the stimuli (Cohen's $d = -0.29$), an effect that was larger for FC/NF pairings (Cohen's $d = -0.25$) than NC/FF pairings (Cohen's $d = -0.12$).

fMRI Study

Behavioral

Replicating the behavioral results in the ERP study, we found that FC resulted in greater d' than NC (M of FC = 2.37 ± 0.89 ; M of NC = 2.01 ± 0.86 ; $t_{16} = 2.52$, $P = 0.02$, $d = 1.26$), indicating that prestimulus threat cues facilitate subsequent threat-related perceptual decisions (Fig. 3A). While the pattern of results for hit rate and false alarm rate were the same as in the ERP study, with a greater hit rate for FC ($M = 0.83 \pm 0.13$) compared with NC ($M = 0.82 \pm 0.14$; Fig. 3B), the difference did not reach statistical significance, possibly due to the smaller number of subjects in the fMRI study. To compare the impact of FC and NC on subsequent FF perception, we also compared the hit rate for FC trials to the correct rejection rate for NC trials ($M = 0.80 \pm 0.10$), however no significant difference was found. We also examined response bias (c) on FC and NC trials. Consistent with the ERP study no difference in bias was found on FC trials ($M = 0.10 \pm 0.48$) and NC trials ($M = -0.04 \pm 0.37$).

RT results are displayed in Figure 3C. A 2 \times 2 repeated-measures ANOVA examining the impact of cue type and stimulus type on RT showed a main effect of cue type ($F_{1,16} = 44.40$, $P = 5.00 \times 10^{-6}$, $\eta^2 = 0.74$), such that FC resulted in faster threat-related perceptual decisions than NC, and an interaction of cue type and stimulus type ($F_{1,16} = 15.84$, $P = 0.001$, $\eta^2 = 0.50$), such that FC resulted in faster identification of FF ($M = 1.42 \pm 0.26$) than NF ($M = 1.62 \pm 0.33$), mean difference = -0.20 , $P = 1.22 \times 10^{-3}$ but the same difference was not seen for NC's impact on FF ($M = 1.71 \pm 0.33$) and NF RT ($M = 1.66 \pm 0.35$). These results are consistent with the behavioral results from the ERP study, and suggest that FC and NC have differential impact on subsequent perception, with only FC enhancing FF detection. These findings were not the result of differences in participant thresholds for fearful versus neutral faces on the threshold task ($t_{16} = 0.75$, $P = 0.46$, $d = 0.38$).

fMRI Results

We first examined the prediction that FC would elicit greater prestimulus activity in a brain region critical for emotional face perception compared with NC. As hypothesized, we found significant STS (left hemisphere, peak MNI coordinates: -44 , -55 , 16 , peak $Z = 4.86$; $P < 0.05$, corrected, right hemisphere, peak MNI coordinates: 42 , -64 , 14 , peak $Z = 4.07$; $P < 0.05$, corrected) activation for FC which was significantly higher than STS activity for NC (peak MNI coordinates: -48 -58 19 ; peak $Z = 2.95$; $P < 0.05$, corrected; Fig. 3D,G). This indicates that FC (but not NC) elicited greater processing in STS in anticipation of a threatening face-related perceptual decision, even before arrival of the face stimulus.

Contrary to our hypothesis similar increases in FC versus NC-elicited activity were not observed in the amygdala. Next, we examined whether the amygdala is sensitive to cue-related effects during stimulus presentation by conducting an analyses of stimulus-related activity using a mixed-model ANOVA with subjects as a random factor and cue type (FC and NC) and stimulus type (FF and NF) as fixed factors. We found a main effect of stimulus type in the amygdala (peak MNI coordinates: -20 1 -16 ; peak $Z = 3.71$; $P < 0.05$, corrected), such that there was greater activity for FF than for NF, and a cue type \times stimulus

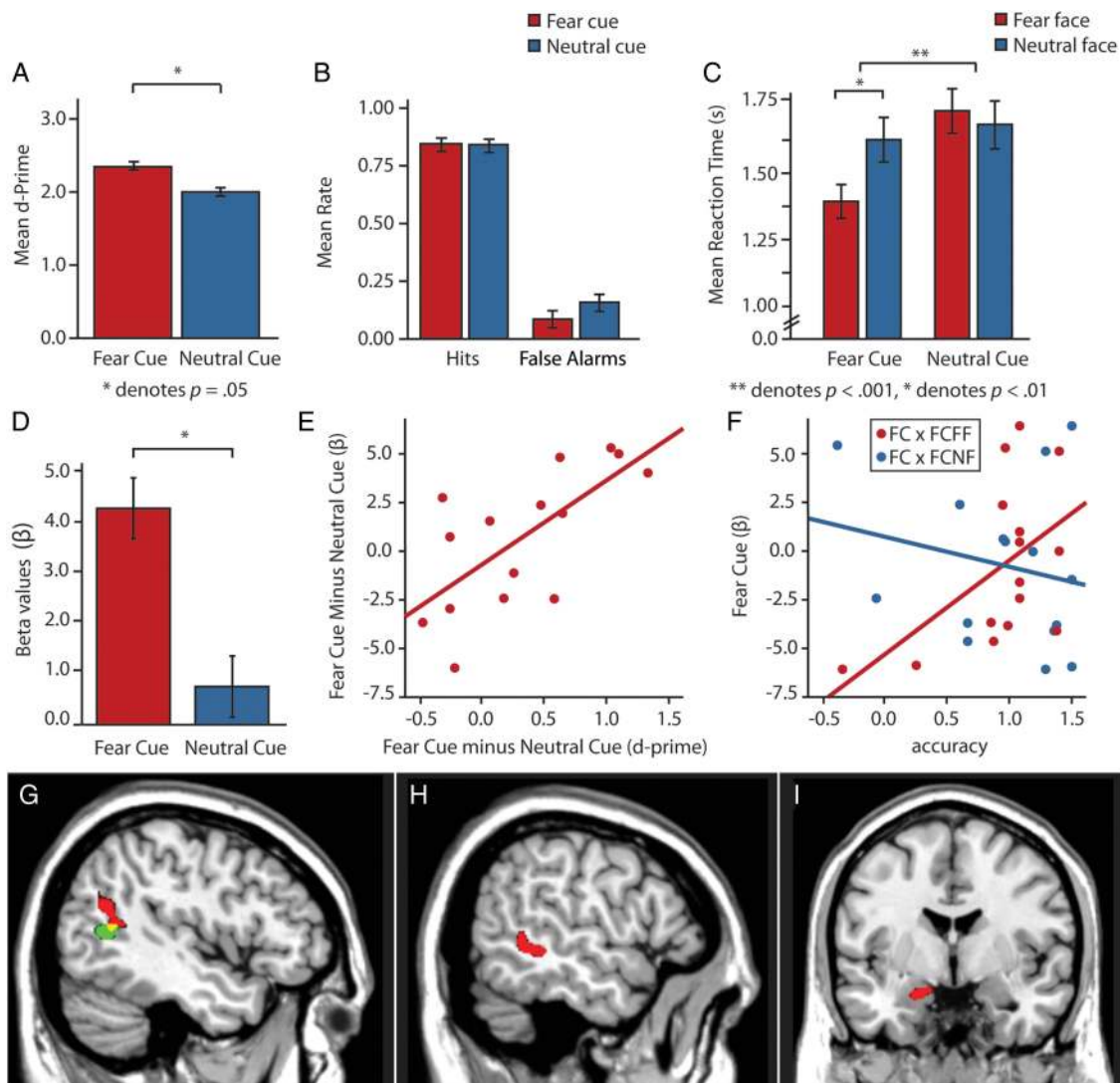


Figure 3. (A) Perceptual sensitivity (measured as d'), for fear and neutral cue trials in the fMRI study. Fear cues resulted in greater perceptual sensitivity than neutral cues. (B) Hit and false alarm rates for fear versus neutral cue trials. Results showed same pattern of differences as ERP study but no significant differences were seen between fear and neutral cue trials in hit rate or false alarm rate. (C) Reaction time for all cue/stimulus combinations. Fear cues resulted in faster perceptual decision-making than neutral cues, with faster identification of fearful than neutral faces, while the same difference was not seen for neutral cues. (D) Fear cue and neutral cue-elicited mean BOLD activity in STS shows greater prestimulus activity for fear versus neutral cues. (E) Greater prestimulus fMRI activity for fear versus neutral cues in STS is associated with improvement in perceptual sensitivity (d') for fear versus neutral cues. (F) Greater activity for fear cues in STS is associated with greater accuracy of subsequently presented fearful faces, but not of neutral faces. (G) Sagittal slice showing greater prestimulus STS activity for fear versus neutral cues (red; left hemisphere) which correlates with improvements in d' for fear versus neutral cues (green). Overlap between the 2 is in yellow. Results are displayed at $P < 0.05$, corrected for multiple comparisons. (H) Sagittal slice showing greater face stimulus-related STS activity for fearful versus neutral faces in the left hemisphere. Results are displayed at $P < 0.05$, corrected for multiple comparisons. (I) Coronal slice showing increased left amygdala activity for fearful versus neutral faces following fear (but not neutral) cues. The cue type \times stimulus type interaction in stimulus-related amygdala activity is displayed at $P < 0.05$, corrected for multiple comparisons.

type interaction (peak MNI coordinates: $-19 -2 -21$; peak $Z = 4.87$; $P < 0.05$, corrected; Fig. 3I). Follow-up paired-sample t -tests conducted within this cluster of activation in the amygdala showed greater activity for FC/FF than for FC/NF (peak MNI coordinates: $-19 0 -18$; peak $Z = 4.60$; $P < 0.05$, corrected), for FC/FF than NC/FF (peak MNI coordinates: $-17 -2 -20$; peak $Z = 4.49$; $P < 0.05$, corrected), and for FC/FF than for NC/ NN, (peak MNI coordinates: $-21 1 -18$; peak $Z = 4.97$; $P < 0.05$, corrected), suggesting that the interaction was driven by increased activity in the FC/FF condition.

Finally, for stimulus-related activity, we observed a main effect of stimulus type in the STS (peak MNI coordinates: $-55 -46 0$; peak $Z = 4.04$; $P < 0.005$, uncorrected; Fig. 3H) such that there was increased activity for FF versus NF and a main effect

of cue type in the FFA (peak MNI coordinates: $-30 -48 -9$; peak $Z = 3.26$; $P < 0.005$; uncorrected), such that there was more FFA activity for all faces following FC compared with NC. Overall, these results demonstrate that the prestimulus presentation of FC had both a general and specific effect on subsequent face processing such that FC boosted the neural processing of all subsequently presented faces in FFA, and only subsequently presented FF in the amygdala.

Relationship Between Cue-related fMRI Activity and Behavioral Performance

We tested the hypothesis that increases in prestimulus STS activity for threat versus neutral cues (Figs 3D,G) relate to improved

threat versus neutral perceptual decision-making across subjects. Results showed that increased STS activity for FC versus NC correlated with subsequent improvement in d' following FC versus NC (peak MNI coordinates: $-49 -47 11$; peak $Z = 4.48$; $P < 0.05$, corrected; Figs 3E,G), demonstrating that the relationship between cue-related activity in STS and subsequent gains in perceptual sensitivity is stronger for threatening cues. These findings indicate a specific relationship between FC elicited activity in a region important in processing emotional expressions and subsequent increases in perceptual sensitivity.

To determine whether there was a specific effect of increased FC-related STS activity on the detection of FF, we examined the relationship between FC-elicited STS activity and accurate identification of FF compared with NF. Results showed that FC-elicited STS activity was more strongly associated with FF than NF accuracy (peak MNI coordinates: $-43 -51 9$; peak $Z = 2.86$; $P < 0.05$, corrected; Fig. 3F). Furthermore, we tested the hypothesis that prestimulus STS activity for threat versus neutral cues relates to improved FC/FF versus NC/FF accuracy. Results showed that the relationship between STS activity for FC and subsequent FF accuracy was stronger than the relationship between NC and subsequent FF accuracy (peak MNI coordinates: $43 -55 11$; peak $Z = 3.02$; $P < 0.05$, corrected), supporting the idea that FC uniquely enhances perception of subsequently presented threatening faces. We did not find a similar correlation between FC-related STS activity and RT.

Our hypothesis focused on the relationship between prestimulus brain activity and subsequent improvement in perception. While amygdala activity was not sensitive to prestimulus cuing (FC versus NC), amygdala activity during FF versus NF stimulus processing was higher following FC versus NC. Due to this significant cue type \times stimulus type interaction in the amygdala, we also examined the possibility that increases in activity in the amygdala for FC/FF would have a significant relationship to behavioral improvements in accuracy or RT, but did not find evidence of this relationship.

Finally, because we found a relationship between prestimulus neural activity and subsequent performance across subjects, we also examined the relationship of cue-related brain activity and subsequent behavior within subjects (across trials). We found that, within subjects, FC activity in the STS ROI correlated with subsequent FF RT more than it correlated with NF RT (peak MNI coordinates: $-52 -55 19$; peak $Z = 3.49$; $P < 0.05$, corrected; peak MNI coordinates: $39 -63 17$; peak $Z = 3.40$; $P < 0.05$, corrected). FC activity in STS also bore a stronger relationship with subsequent FF RT than NC activity did with FF RTs that followed (peak MNI coordinates: $-52 -60 15$; peak $Z = 3.40$; $P < 0.05$, corrected). These results show that increases in FC-related activity in STS specifically speed subsequent FF RT on that trial.

Discussion

The present study examined whether prior threat-related information enhances perceptual decision-making more than prior neutral information. Behaviorally, we established in 2 experiments that threat-related cues enhance both sensitivity and speed of subsequent threat-related perceptual decision-making more than neutral cues enhance neutral decision-making. Furthermore, in a separate behavioral study we showed that salient but positively valenced happy cues did not lead to improved perceptual sensitivity, indicating that threat-related information specifically enhances the sensitivity of subsequent perceptual decision-making. Neurally, even before face stimuli were presented, threat-related cues resulted in increased LPP and STS

activity, both of which are measures of emotional face processing. Increased prestimulus activity for threat versus neutral cues was associated with subsequent gains in threat-related perceptual decision-making, both across subjects and across trials within subjects, more so for threatening than neutral faces. Threat cues also resulted in greater FFA activity for fearful and neutral faces, but increased amygdala activity for fearful faces only. In a literature focused primarily on the importance of automatic processing of threatening stimuli, the present results establish the importance of top-down factors and the role of prestimulus neural processing in understanding the perceptual prioritization of threatening information. Additionally, these results contradict findings suggesting that neural processing of threatening faces is prioritized regardless of top-down influence (Vuilleumier et al. 2001), and are in line with the view that enhanced visual processing of emotional stimuli is strongly influenced by top-down factors (Pessoa et al. 2002; Hahn and Gronlund 2007; Pessoa and Adolphs 2010; Mohanty and Sussman 2013).

We used a perceptual discrimination task that was made challenging by degrading threatening and neutral faces to subject-specific perceptual thresholds, encouraging the use of cue-related information in perceptual decision-making. Threatening and neutral faces were equally likely to follow each cue; hence, differences in behavior and brain activity were likely due to the perceptual “sets” utilized by subjects to make decisions regarding fearful or neutral faces. Finally, threatening and neutral faces were matched for luminance and spatial frequency, minimizing the contribution of low-level confounds. In both the ERP and fMRI study, threat compared with neutral cues boosted the perceptual sensitivity of subsequent threat-related perceptual decisions. Threat cues specifically enhanced perception of threatening faces, speeding their detection compared with neutral faces. Neutral cues did not show the same specific effect, supporting the idea that threat cues may encourage the use of threat-specific perceptual templates that enhance subsequent decision-making. Although earlier studies have demonstrated the enhancing effect of prior threatening stimuli on general perception (Phelps et al. 2006; Bocanegra and Zeelenberg 2009), our study is important in demonstrating that cues indicating a threat-related decision enhance the sensitivity of subsequent perceptual decisions.

Examination of ERP and fMRI activity in response to both cues and faces, suggests a mechanism by which prior information facilitates perception. Greater LPP and STS activation for threatening versus neutral faces is in line with earlier studies showing LPP (Holmes et al. 2009) and STS (Hasselmo et al. 1989; Sugase et al. 1999) involvement in perceptual processing of emotional faces. However, increased LPP and STS activation for threatening versus neutral “cues” suggests that neural processes involved in perception of threatening faces are employed even when anticipating threat-related perceptual decisions and are different than when anticipating neutral faces. Furthermore, in a separate behavioral study we showed that salient but positively valenced happy cues did not lead to improved perceptual sensitivity, indicating that threat-related information specifically enhances the sensitivity of subsequent perceptual decision-making. While earlier studies have shown that prestimulus cues indicating subsequent appearance of a face result in greater activity in face-sensitive regions (Puri et al. 2009), our study shows that cues indicating a threatening face decision engage neural mechanisms involved specifically in processing emotional aspects of faces (LPP and STS activity).

Importantly, we found that increases in prestimulus LPP activity for threat cues predicted improved sensitivity for

threat-related perceptual decision-making and more accurate detection of threatening compared with neutral stimuli. Similarly, increases in prestimulus STS activity for threat versus neutral cues predicted improved sensitivity of threat versus neutral decision-making as well as more accurate detection threatening versus neutral stimuli. Furthermore, threat cues did not enhance “neutral” stimulus-related processing, as measured by the LPP or by increased processing in the STS or the amygdala. Together, these findings support the specific enhancing effect of prestimulus threat-related brain activity on subsequent threat-related perceptual decisions. These specific findings align with studies showing that high arousal emotions like fear and disgust have distinct effects on perception (Krusemark and Li 2011; Nicol et al. 2013) and contradict a more general enhancing effect of arousal on low-level perceptual qualities like contrast sensitivity or spatial frequency (De Cesarei and Codispoti 2013; Lee et al. 2014).

Although we did not find greater threat cue-elicited activity in the amygdala, we did find that threat cues enhance amygdala processing of threatening versus neutral stimuli, suggesting that threat cues have a more significant impact on amygdala activity during stimulus processing than during cue presentation. However, while threat cue-elicited increases in STS activation predicted improvement in perception, increased processing of threatening faces following threatening cues in the amygdala did not predict improved accuracy or RT. These findings are consistent with the view that STS is important for the perception of the dynamic aspects of faces, specifically emotional expressions; whereas the amygdala is part of an extended network that processes emotional information gleaned from face perception and directs attention to threatening faces (Haxby et al. 2000; Vuilleumier 2005). According to these proposed roles of STS and the amygdala, STS would have greater involvement in making perceptual decisions regarding emotional faces, while the amygdala would play a greater role in identifying the salience of and directing attention to a presented emotional face.

Threat-specific prestimulus information can enhance subsequent perceptual decisions via several mechanisms. Increased prestimulus activity may reflect increased attention prior to stimulus onset which improves subsequent detection by biasing sensory processing in favor of the attended location or feature (Desimone and Duncan 1995). Attention-related increases in prestimulus activity are observed in cortical areas that code attended locations (Kastner et al. 1999; Hopfinger et al. 2000) or features (Chawla et al. 1999; Shulman et al. 1999; Giesbrecht et al. 2006; Serences and Boynton 2007; Stokes et al. 2009), and we present evidence that similar prestimulus increases are observed for regions coding threat-related features such as STS for emotional expressions. According to arousal-biased competition theory, threat cues may increase arousal, biasing selective attention toward perception of the stimuli relevant to the goal at hand (Mathier and Sutherland 2011). This attentional bias may occur as a result of the arousal-induced release of norepinephrine into the locus coeruleus leading to increased levels of glutamate and norepinephrine at the site of the goal-relevant representation, thereby enhancing the representation of the goal-relevant stimulus (Mather et al. 2015).

Alternatively, according to sequential sampling models of perceptual decision-making such as the drift diffusion model (Ratcliff 1978; Ratcliff and Smith 2004), increases in prestimulus activity may reflect a shift in the starting point for evidence accumulation toward a specific decision, a change in the rate of evidence accumulation, or a combination of both (Bode et al. 2012; Summerfield and de Lange 2014). Evidence demonstrating that

enhancing input increases the rate of evidence accumulation (Huk and Shadlen 2005) is consistent with the possibility that increased activity prior to stimulus presentation influences subsequent choices by increasing the rate at which evidence drifts toward the decision bound (Summerfield and de Lange 2014). Since a faster drift rate is associated with faster and more accurate responses (Ratcliff and McKoon 2008), it is possible in the present study that prestimulus increases in LPP and STS activity for threat cues enhance subsequent accuracy, perceptual sensitivity, and RT by affecting the rate of evidence accumulation in the decision-making process.

The predictive coding hypothesis provides another neurobiologically plausible mechanism by which prestimulus information can aid perceptual decision-making (Gregory 1980; Mumford 1992). According to this theory, prior to physical contact with a stimulus, the brain generates a perceptual template of likely or relevant stimuli, against which incoming sensory information is matched, facilitating perception of the anticipated stimulus (Dayan et al. 1995; Doshier and Lu 1999; Rao and Ballard 1999; Summerfield and Koechlin 2008; Zelano et al. 2011). In our study, it is possible that perceptual templates maintained in prefrontal regions (Summerfield et al. 2006) sensitize STS for accumulating evidence regarding emotional faces via connectivity of STS with prefrontal regions (Gschwind et al. 2012; Zhen et al. 2013). While both STS and FFA are considered part of the core face processing system, studies of anatomical and functional connectivity suggest that only surprisingly weak connections between these 2 regions exist (Gschwind et al. 2012; Pyles et al. 2013; Zhen et al. 2013). However, studies demonstrate connectivity between the STS and amygdala (Davies-Thompson and Andrews 2012; Foley et al. 2012), which could facilitate the preferential processing of fearful faces following threat-related cues.

In line with the predictive coding hypothesis, multivariate pattern analyses of prestimulus ensemble patterns of fMRI data showed that target-specific ensemble patterns emerge prior to encounter with the target stimulus in prefrontal and sensory cortices and these prestimulus patterns reliably predict behavioral performance (Zelano et al. 2011). Similarly, ensemble activity patterns of BOLD signal showed that top-down attention to a target activates target-specific representations in visual areas, indicating a preparatory bias favoring the attended over competing stimuli (Peelen et al. 2009; Stokes et al. 2009). While these studies demonstrate that the brain represents a relevant stimulus prior to its onset and that this representation facilitates perception, it is unclear whether and how perceptual representation for a threatening stimulus is superior to a neutral stimulus and whether this accounts for its prioritized perception. Since presentation of more specific information is hypothesized to yield more precise search templates ultimately resulting in better target detection (Schmidt and Zelinsky 2009), it is possible that threat cues may produce more specific templates than neutral cues, resulting in better detection of upcoming stimuli.

The importance of top-down factors is well established in the perception literature. For example, rainbows are composed of a continuous range of colors but are experienced as a set of distinct colors because we use pre-existing conceptual boundaries to divide the continuous spectrum of light into categories. While the role of top-down factors in the perceptual categorization of emotional stimuli has been recognized (Brosch et al. 2010; Pessoa and Adolphs 2010), ours is the first study to demonstrate that threatening compared with neutral prestimulus cues can lead to enhanced anticipatory neural processing, enhanced stimulus-related processing, and improved precision in stimulus detection. By shifting the emphasis from stimulus-driven to top-

down factors in the perceptual prioritization of emotional stimuli, the present findings underscore the need to include top-down emotion-related processing in existing models of emotion-perception interactions.

Finally, top-down processes play an important role in the development and maintenance of anxiety via distorted expectations and goals, as well as through threat-related schemata (Beck 1976; Mogg et al. 1989). For individuals with anxiety, expectations of aversive future events are exaggerated and often inaccurate, affecting a range of functions from basic sensory processes to higher-level cognition (Grupe and Nitschke 2013). It has been hypothesized that trait anxiety and induced anxiety may have additive enhancing effects on sensory-perceptual functions (Robinson et al. 2013). We recently showed that for individuals higher in trait anxiety, situationally induced anxiety resulted in greater perceptual sensitivity following threatening versus neutral cues, demonstrating the importance of prior information in facilitating threat perception in anxiety (Sussman et al. 2015). Because hypervigilance, expectations, and predictability of future threats are key factors in the elicitation of anxiety (Davis et al. 2010; Grupe and Nitschke 2013), further research examining the impact of the expectation of threat on perception will contribute both to a more comprehensive understanding of normal emotion-perception interactions and to our understanding of the development and maintenance of anxiety.

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