Different brain activity in response to emotional faces alone and augmented by contextual information

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Abstract

This study examined the extent to which emotional face stimuli differ from the neural reactivity associated with more ecological contextually augmented stimuli. Participants were scanned when they viewed contextually rich pictures depicting both emotional faces and context, and pictures of emotional faces presented alone. Emotional faces alone were more strongly associated with brain activity in paralimbic and social information processing regions, whereas emotional faces augmented by context were associated with increased and sustained activity in regions potentially representing increased complexity and subjective emotional experience. Furthermore, context effects were modulated by emotional intensity and valence. These findings suggest that cortical elaboration that is apparent in contextually augmented stimuli may be missed in studies of emotional faces alone, whereas emotional faces may more selectively recruit limbic reactivity.

Descriptors: fMRI, Context, Faces, Emotional intensity, Valence

Pictures of nonfamous facial expressions have been widely used as stimuli in examining the role of the subcortical-limbic regions, especially the amygdala, in emotional information processing (Kesler-West et al., 2001; Matsuda et al., 2013; Phillips et al., 1998, 2001; Yang et al., 2002). A frequent claim is that face stimuli are a proxy for social information processing. However, face stimuli, as used in fMRI, are often nonecological (e.g., background removed, hair cropped, disembodied), to the point that subjects frequently describe experimentally defined neutral faces as "weird," "eerie," or "scary," and rate them as negative (Tottenham, Phuong, Flannery, Gabard-Durnam, & Goff, 2013). Possibly, brain processes unique to disembodied nonfamous face processing might occur because these stimuli lack meaningful contextual features that pervade real-world visual stimuli (e.g., hair, environment, other people). To understand the generalizability of disembodied nonfamous faces as social stimuli, this study compared processing of faces without context to the same face stimuli augmented by relevant contextual features.

Our theory is that ecological contextual processing is more of a neocortical process that involves appraisal in addition to basic face recognition, qualifying perception of low-level information. Initial evidence supports this theory. For example, semantically congruent contexts enhance recognition of facial expressions (Righart & de Gelder, 2008b; Zagorska, 1987). Electrophysiological studies suggest that emotional contexts affect early stages of face processing in the left temporal and occipital regions (Righart & de Gelder, 2006, 2008a). Interactive processing of emotional faces and congruent background information has been observed in the visual cortex (Van den Stock, Vandenbulcke, Sinke, Goebel, & de Gelder, in press). Preceding or primed contextual information also affects neural features of perception of subsequently presented faces or attribution of mental states for face processing (Kim et al., 2004; Mobbs et al., 2006; Schwarz, Wieser, Gerdes, Muhlberger, & Pauli, 2013). Recent reviews thus highlight the importance of considering context in order to understand everyday perceptual processing of faces (Barrett, Mesquita, & Gendron, 2011; Hassin, Aviezer, & Bentin, 2013; Wieser & Brosch, 2012). However, it is unclear whether meaningful contextual information (e.g., situation-specific cues, backgrounds) affects subjective emotional responses and neural activity in response to facial expressions above and beyond the congruent emotions in those expressions themselves. Thus, this study focused on whether congruent contextual information influences subjective emotional and neural responses to emotional faces.

Consistent with our model, initial neuroimaging data suggests that facial expressions and more complex emotional pictures may differentially recruit brain networks associated with rapid and elaborative emotional information processing. Emotional processing of faces appears to rely on quick automatic processing (Ekman, 1999) through the subcortical-limbic pathways (LeDoux, 1996). Consistent with these accounts, neuroimaging studies using disembodied nonfamous emotional faces without context have

demonstrated expression-related activity in the amygdala (e.g., Adolphs, 2002; Lange et al., 2003; Whalen et al., 1998) and paralimbic regions, including the anterior insula, orbitofrontal cortex (OFC), and posterior cingulate cortex (PCC) (e.g., Blair, Morris, Frith, Perrett, & Dolan, 1999; Moriguchi et al., 2005; Phillips et al., 1998; Whalen et al., 2001). Furthermore, face processing has been associated with relatively early neural activity, which may be an index of automatic processing of faces (for a review, see de Gelder et al., 2006).

In contrast, contextually rich emotional pictures may be processed through cortical pathways associated with higher-level elaborative processing such as appraisal and semantic evaluation of emotional information (e.g., Clore & Ortony, 2000; Lazarus, 1991). Consistent with these accounts, contextually rich emotional pictures (e.g., International Affective Picture System, IAPS) provoke activity in a widespread network of prefrontal and limbic regions including the amygdala, thalamus, hippocampus, hypothalamus, medial prefrontal cortex (MPFC), OFC, and visual cortex (e.g., Garavan, Pendergrass, Ross, Stein, & Risinger, 2001; Grimm et al., 2006; Murphy, Nimmo-Smith, & Lawrence, 2003; Northoff et al., 2000; Sabatinelli et al., 2011). Evidence also suggests that semantic elaboration and appraisal of contextual information may be associated with late and sustained processing (for a review, see de Gelder et al., 2006).

To yield an additive design that tests our theory, it was essential and novel to present pictures of facial expressions, along with the more ecological pictures containing contexts from which they were taken, in the same experiment. Previous studies comparing brain activation in response to facial expressions and complex emotional pictures (Britton, Taylor, Sudheimer, & Liberzon, 2006; Geday, Gjedde, Boldsen, & Kupers, 2003; Schafer, Schienle, & Vaitl, 2005) yielded different networks. For example, emotional faces provoked greater brain activation in the superior temporal gyrus (STG), insula, and anterior cingulate cortex (ACC) relative to emotional pictures, whereas emotional pictures more strongly activated only visual cortex. However, these studies could not make claims regarding additive effects given that the same faces were not present in the picture stimuli. They also included relatively simple IAPS pictures such as animals and guns (Britton et al., 2006; Schafer et al., 2005). The degree of complexity in these simple facial expressions and animal IAPS pictures may be similar, yielding a nonadditive design.

We used emotional pictures containing both emotional faces and contextual information selected from the well-validated IAPS as a naturalistic corpus and new pictures containing just the facial expressions from these same pictures. This approach allows us to test the primary question of whether imaging studies using emotional faces alone preserve features of more ecological stimuli that include faces and what is different about how the more ecological stimuli are processed.

We also attended to possible moderation by emotional factors known to modulate brain function including emotional intensity (defined as how positive or negative the subject reported feeling compared to a neutral rating), arousal, and valence (categorized as positivity vs. negativity in this study; e.g., Anderson et al., 2003; Touroutoglou, Hollenbeck, Dickerson, & Barrett, 2012). We assessed emotional intensity and arousal separately because relationships between these constructs vary as a function of context (e.g., personality and situations; Kuppens, Tuerlinckx, Russell, & Barrett, 2013). Emotional intensity is consistently differentiated from arousal and valence (for a review, see Barrett, Mesquita, Ochsner, & Gross, 2007), so both constructs were included.

In summary, we addressed three specific questions: (1) Do emotional faces augmented by contextual information provoke more affectively intense emotions (e.g., more negative or positive or more arousing) than emotional faces presented alone? (2) Do emotional faces augmented by contextual information additionally recruit a wider brain network, compared to emotional faces presented alone? and (3) Are contextual effects qualified by emotional intensity, arousal, and valence? We hypothesized that emotional faces augmented by contextual information would be rated as more affectively intense compared to faces presented alone. Our primary hypothesis is that emotional faces presented in meaningful contexts would activate a wider brain network, particularly including prefrontal and limbic regions associated with cognitive appraisal and subjective emotional experience, whereas facial expressions presented alone would activate subcortical-limbic and temporal (e.g., STG) regions associated with emotional face processing. Furthermore, we predicted that emotional faces presented with contextual information would show late and sustained neural activity, while faces presented alone would show early neural activity reflecting different time courses of neural reactivity associated with feedback in brain responses to the stimuli.

Additionally, we considered the potential for moderation effects such that prefrontal (e.g., MPFC/ACC) and limbic regions (e.g., amygdala and caudate) would be modulated by emotional intensity (Anderson et al., 2003; Dolcos, LaBar, & Cabeza, 2004; Grimm et al., 2006; Small et al., 2003) and arousal (Gerdes et al., 2010; Lewis, Critchley, Rotshtein, & Dolan, 2007; Viinikainen et al., 2010), and prefrontal regions (e.g., VMPFC/OFC and ventrolateral prefrontal cortex [VLPFC]) and limbic regions (e.g., insula and amygdala) would be modulated by emotional valence (e.g., Anders, Eippert, Weiskopf, & Veit, 2008; Anders, Lotze, Erb, Grodd, & Birbaumer, 2004; Gerdes et al., 2010; Royet, Plailly, Delon-Martin, Kareken, & Segebarth, 2003). Findings of how emotional faces with contextual information are differently processed compared to faces presented alone may contribute to a better understanding of how people process emotional information (e.g., faces and situational contexts presented together) in social situations of everyday life, for example, as a function of contextual appraisal. These data may help to put the large literature on disembodied, hairless, noncontextual faces prominent in the fMRI world in an interpretable context.

Method

Subjects

Twelve subjects participated in this study.[1] One subject was excluded due to an administrative problem. Thus, eleven healthy, right-handed subjects (3 male, 6 Caucasian, $M (SD)_{age} = 36.55$ (10.74), $M (SD)_{education} = 15.82$ (1.89)) were included in data analyses. Subjects had no current or historical Axis I psychiatric disorder as assessed by the Structured Clinical Interview for DSM-IV diagnosis (First, Spitzer, Gibbon, & Williams, 1996), or self-reported neurological disorders. All subjects signed a written consent form approved by the University of Pittsburgh's Institutional Review Board.

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1. These healthy subjects also were recruited as the control group for a study on patients with major depression in which the age of depressed subjects ranged from late teens to early 50s and the female-male ratio was approximately 2:1, so the age and the female-male ratio of healthy subjects were matched with those of depressed subjects.

Figure 1. Example of FACE and FACE+CONTEXT stimuli.

Emotional Stimuli

A large corpus of affective pictures from the IAPS (Lang, Bradley, & Cuthbert, 2001) was roughly classified into four groups; FACE, NO FACE, FACE+CONTEXT, and OTHERS. Pictures containing perceivable faces as well as other emotionally congruent contextual information and backgrounds were categorized into the FACE+CONTEXT group by two raters (171 pictures, $\kappa = .85$, $p < .0001$). From this set, 15 positive and 15 negative emotional pictures were selected that had uniformly high or low normative valence ratings,[2] M (SD) $_{positive} = 7.22$ (0.48) and M (SD)$_{negative} = 2.82$ (0.60); $F(1,28) = 489.92$, $p < .0001$, $\eta^2 = 0.95$. The majority of positive emotional pictures depicted happy social situations, while negative emotional pictures depicted sad and other negative (e.g., anger, fear, and disgust) situations (see online supporting information S-I). Corresponding emotional face stimuli were created from each emotional picture (15 positive and 15 negative) by cutting just the face out of these whole pictures and enlarging it to a size comparable to the original picture. In pictures with more than one face, we selected the face that was the most emotionally salient or centrally positioned. The enlarged face was placed on a gray background, consistent with most other neuroimaging studies of facial expressions. All stimuli were converted to grayscale and balanced for mean luminance and size in order to equate psychophysical characteristics across conditions (see Figure 1).

Experimental Paradigm

A slow event-related design was employed to prevent amygdala habituation effects associated with fast presentation of emotion-provoking stimuli and to allow examination of the time course of event-related responses. Subjects were presented with randomly ordered stimuli of emotional faces augmented with contextual information or emotional faces alone for 6 s, followed by a 6-s

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2. The numbers of the selected pictures from the IAPS were the following: positively valenced pictures (2040, 2303, 2340, 2370, 2391, 2530, 4532, 4603, 4700, 7325, 8330, 8350, 8461, 8497, 8540), and negatively valenced pictures (2205, 2312, 2590, 2661, 2691, 2700, 2900, 3220, 3300, 6312, 6313, 6836, 9250, 9421, 9530).

fixation cross. Subjects were instructed to press a button as soon as possible when the stimulus appeared on the screen. We used this simple button press task to encourage subjects to maintain attention to each stimulus, without directing them to specific features of the stimulus. We did not use any instructions related to implicit or explicit emotional tasks to prevent emotion-regulation effects associated with accomplishing a cognitive task (e.g., Lange et al., 2003). After the scan, subjects were asked to evaluate their subjective emotional responses (i.e., valence and arousal) to each emotional stimulus using a Self-Assessment Manikin (SAM; Lang, 1980), consisting of graphic icons depicting values on a continuously varying scale reflecting emotional reactions.

Image Acquisition and Preprocessing

Imaging acquisition. Images were acquired on a 3T GE Signa scanner (General Electric, Milwaukee, WI). Thirty 3.2 mm slices were acquired parallel to the AC-PC line with a reverse spiral pulse sequence (T2*-weighted imaged depicting BOLD signal; TR = 1,500 ms, TE = 26 ms, FOV = 20 cm, flip angle = 60°). Each image was acquired in 1.5 sec, allowing 8 scans per trial. Thirty-four continuous, T1-weighted, 3.2 mm slices parallel to the AC-PC line were collected as structural images.

fMRI data preprocessing. fMRI analyses were conducted using locally developed Neuroimaging Software (Fissell et al., 2003) and AFNI (Cox, 1996). Motion artifacts were corrected via a 6-parameter linear transformation using Automated Image Registration (AIR; Woods, Mazziotta, & Cherry, 1993). Trials containing scans with greater than 5 mm movement (5° rotation) from the first image or 1 mm movement (1° rotation) from the previous scan were excluded from statistical analysis. Linear trend overruns were removed to eliminate effects of scanner drift, outliers > median ± 2.2I interquartile range (IQR) were Winsorized (i.e., rescaled to median ± 2.2I IQR), and fMRI data were temporally smoothed (five-point middle-peaked filter) to obtain time courses representing plausibly smooth hemodynamic responses rather than transient noise. Images were cross-registered to a reference brain from the study using the 12-parameter linear AIR algorithm and spatially smoothed (6 mm full width half maximum three-dimensional Gaussian kernel).

fMRI Data Analyses

We used model-free analyses to account for empirical variation in the shape of the hemodynamic response (e.g., sustained activity at 8.5–12 s after the onset of emotional stimulus) rather than relying on hemodynamic responses to have a canonical shape (e.g., as we have done for similar designs in Siegle, Thompson, Carter, Steinhauer, and Thase [2007]). The long duration of each trial implemented in our slow event-related design enabled us to use scan-within-trial (defined as a time factor) as a repeated measure, eliminating the need for potentially misleading event deconvolution.

Effect of augmentation of faces with context. Our primary hypothesis was evaluated within a voxelwise Context (FACE+CONTEXT vs. FACE) × Time (8 scans of 0–12 s in each trial) random effects analysis of variance (ANOVA) with subject as a random factor, and context and time as fixed factors. To control for temporal autocorrelation, brain regions were further subjected to mixed effects analyses of signal change using context and time

as repeated measures and subject as a random factor, assuming an AR1 covariance structure using restricted maximum likelihood estimation (REML).

Context effects qualified by subjective emotional intensity and arousal. To test whether contextual effects were qualified by subjective emotional intensity, we first compared subjective emotional reactions between the same pictures of faces alone and augmented by contextual information. We divided pictures into two groups based on participants' subjective emotion ratings: (1) pictures with different emotional intensity (emotional intensity difference range = 1–4) between FACE+CONTEXT and FACE (unmatched group: FACE+CONTEXT > FACE in emotional intensity), and (2) pictures with the same emotional intensity between FACE+CONTEXT and FACE (matched group: FACE+CONTEXT = FACE in emotional intensity, thus intensity difference = 0). The average number of pairs of pictures across participants for which emotional intensity of faces differed from faces augmented with context was 14 (out of 30 pairs [47%]) (unmatched group). The average number of pairs of pictures across participants for which emotional intensity of faces perfectly matched those for faces augmented with context was 13 (out of 30 pairs [43%]) (matched group). Testing interactions between Context × Emotional Intensity (unmatched vs. matched) × Time allowed us to examine whether contextual effects would be salient when faces presented with contextual information provoked more intense emotions than faces alone. To do this, time courses in brain regions showing greater activation in faces presented with context compared to faces presented alone pictures were extracted and tested by mixed effects analyses with subject as a random factor and context (FACE+CONTEXT vs. FACE), emotional intensity (unmatched vs. matched), time (8 scans of 0–12 s in each trial) as fixed factors, assuming an AR covariance structure using REML. We also performed the analogous mixed effects analyses using arousal ratings to test whether contextual effects were qualified by subjective arousal ratings (see supporting information S-II).

Context effects modulated by valence. To further explore the possibility that context effects were modulated by valence, we performed a Context × Valence (positive vs. negative) × Time ANOVA, again with subject as a random factor, and context, valence, and time as fixed factors, subjected to empirically derived contiguity thresholding as described below.

Type 1 error control. Main effects and interaction maps of context and emotional factors were thresholded at uncorrected $p < .005$. To control Type 1 error at $p < .05$ across the whole brain for each family of tests (i.e., less than 5% chance that even one voxel was identified in error), voxelwise tests at a given statistical threshold were subjected to empirically determined contiguity thresholds based on the spatial autocorrelation of statistical maps using AFNI's AlphaSim program. Thus, both the uncorrected p value and contiguity threshold necessary to achieve a corrected brainwise $p < .05$ are reported with each test described above.

Temporal characteristics of brain activity. We explored time courses of brain activity to characterize different temporal dynamics of brain activity in regions associated with processing faces presented with contextual information and faces alone, and modulated by valence. Time courses between different conditions were compared at each TR (scan) to identify temporal regions showing

significant condition-related differences in activity. Guthrie & Buchwald's (1991) method was used to control Type I error by identifying how long an interval was necessary to interpret a window of differences as significant at $p < .05$, thus implementing a "temporal contiguity threshold," similar to the spatial contiguity thresholds used in other fMRI analyses (described in supporting information S-III). Significant temporal windows are highlighted below the x axis of each time course figure. We also defined early activity as the latter 3 s of the period during which the picture stimulus was on screen (3–6 s in each trial) and late activity as the latter 3 s of the period during which the pictures stimulus was off screen and the fixation was on screen (9–12 s in each trial), similarly used in previous studies (Siegle et al., 2007; Silk et al., 2007).

Results

Post-Scan Subjective Ratings for Question 1: Do Emotional Faces Augmented by Contextual Information Provoke More Affectively Intense Emotions than Emotional Faces Presented Alone?

To answer this question, we analyzed both emotional intensity and arousal ratings. Emotional intensity was determined as the absolute value of deviation of the SAM valence score (range from 1 *positive* to 9 *negative*) of each picture from a neutral score (5); for example, valence scores of either 4 or 6 would each have an intensity of 1. A two-way ANOVA was conducted on emotional intensity with the repeated measures factors of context (FACE+CONTEXT vs. FACE) and stimulus valence (positive vs. negative). The main effect of context was significant, $F(1,10) = 21.27$, $p < .001$, $\eta^2 = .68$, and not affected by stimulus valence, $F(1,10) = 0.33$, $p > .50$. As predicted, emotional faces presented with context, M (SD) = 3.09 (0.19), were rated as more affectively intense (more positive or negative) than faces alone, M (SD) = 2.28 (0.30). For arousal ratings, the analogous ANOVA revealed a significant Context × Stimulus Valence interaction effect, $F(1,10) = 11.92$, $p < .01$, $\eta^2 = .54$. Emotional faces augmented with contextual information, M (SD) = 7.06 (1.14), were rated as more arousing than faces alone, M (SD) = 6.11 (0.80), only in the negative condition, but not in the positive condition (FACE+CONTEXT: M (SD) = 4.84 (2.06); FACE: M (SD) = 4.70 (1.83)).

fMRI Results for Question 2: Do Emotional Faces Augmented by Contextual Information Additionally Recruit a Wider Brain Network, Compared to Emotional Faces Presented Alone?

A wide network of expected primarily limbic and social brain regions was activated by both faces alone and faces augmented with contextual information (see S-IV). To address regions that were more strongly activated in one context or the other, a Context (FACE vs. FACE+CONTEXT) × Time (TR) random effects ANOVA indicated significant Context × Time interaction effects in brain regions associated with emotion processing ($p < .005$, 36 voxels contiguity; Table 1, Figure 2). Faces augmented by contextual information engaged a widespread network including prefrontal and occipital regions. Of particular interest, activity in the left LPFC (BA10/47) (6–12 s: $F(1,10) = 13.09$, $p < .001$, $\eta^2 = .57$) and MPFC (BA10/11) were larger and more sustained in response to faces augmented with context compared to faces presented alone (7.5–12 s: $F(1,10) = 22.81$, $p < .001$, $\eta^2 = .69$) (Figure 3a and 3b). In contrast, facial expressions more strongly

Table 1. *Regions with Significant Interactions of Context (FACE+CONTEXT vs. FACE) × Time*[a]

Region	BA	Size	Max *F*	Talairach coordinate		
				x	*y*	*z*
FACE+CONTEXT > FACE						
Medial frontal gyrus (VMPFC)	10/11/32	601	7.79	9	37	−15
Orbital gyrus	11	100	5.71	11	34	−27
Middle frontal gyrus (LPFC)	47/10	1803	12.44	−33	46	−3
Inferior frontal gyrus	11	86	6.84	14	35	−20
Middle frontal gyrus	11	441	6.3	24	38	−13
Inferior occipital gyrus	18	3459	13.07	37	−84	−8
Inferior occipital gyrus	18	505	7.16	−23	−90	−7
Inferior temporal gyrus	37	165	5.34	−52	−67	−2
Middle occipital gyrus	18/19	1183	8.33	−28	−84	6
Cuneus	17	212	5.14	22	−79	9
Cuneus	17	617	8.86	−17	−94	2
Declive	−	3630	12.01	36	−74	−20
Declive	−	261	7.76	−53	−59	−21
FACE > FACE+CONTEXT						
Posterior cingulate gyrus (PCC)	23	307	7.5	−2	−35	22
Cingulate gyrus	31/23	3892	8.44	3	−26	34
Insula	13	225	4.88	−36	10	−3
Precuneus	7	440	8.7	−12	−45	54
Paracentral lobule	5	896	10.69	−9	−38	55
Medial frontal gyrus	6	556	5.45	2	−19	55
Superior temporal gyrus	39	941	7.69	52	−57	23
Supramarginal gyrus	40	1043	6.92	55	−52	29
Parahippocampal gyrus	35	236	4.84	32	−15	−17
Thalamus	−	18	3.95	22	−22	6
Caudate	−	24	5.14	36	−15	−9

Note. BA = Brodmann area; Size = number of voxels; Max *F* = maximum *F* value.
[a]$p < .005$, 36 voxels contiguity.

engaged activity in limbic/paralimbic regions and temporal/parietal regions (e.g., pSTG extending to the supramarginal gyrus and precuneus) associated with emotional and face processing. Of particular interest, activity in paralimbic regions including the PCC (BA23/29) (3–12 s: $F(1,10) = 16.20$, $p < .001$, $\eta^2 = .62$) and the left anterior insula (BA13) (4.5–12 s: $F(1,10) = 5.82$, $p < .05$,

Figure 2. Shared and dissociable brain networks associated with FACE and FACE+CONTEXT.

$\eta^2 = .37$) showed greater in response to faces presented alone compared to faces presented with contextual information (Figure 3c and 3d).

fMRI Results for Question 3: Are Contextual Effects Qualified by Emotional Intensity, Arousal, and Valence?

Activity associated with contexts qualified by subjective emotional intensity and arousal. For emotional intensity, mixed effects analysis showed a significant Context × Emotional Intensity interaction effect in the MPFC, $F(1,319.93) = 12.20$, $p < .01$, $\eta^2 = .04$. Interaction effects with time were not found, $F(7,264.90) = .65$, $p > .70$. Pairwise comparisons showed that there was a significant difference in MPFC activation between faces presented with context and faces alone when emotional intensity was greater in faces presented with context compared to faces alone, $t(10) = 3.44$, $p < .01$, $d = 1.04$ (Figure 4a, unmatched group), but not when emotional intensity was the same between faces with context and faces alone, $t(10) = .64$, $p > .50$ (Figure 4a, matched group). The Context × Emotional Intensity interaction effect in the left LPFC was not significant, $F(1,309.37) = 2.88$, $p > .08$, but the context main effect was significant, $F(1,317.57) = 48.57$, $p < .001$, $\eta^2 = .13$. Regardless of emotional intensity (both unmatched and matched groups), the LPFC showed greater reactivity to faces presented with context than faces presented alone (Figure 4b). For arousal ratings, the analogous mixed effects analyses revealed that there were no significant Context × Arousal interaction and Context × Arousal × Time interaction effects in the MPFC and LPFC, thus these results were not further considered (see S-II).
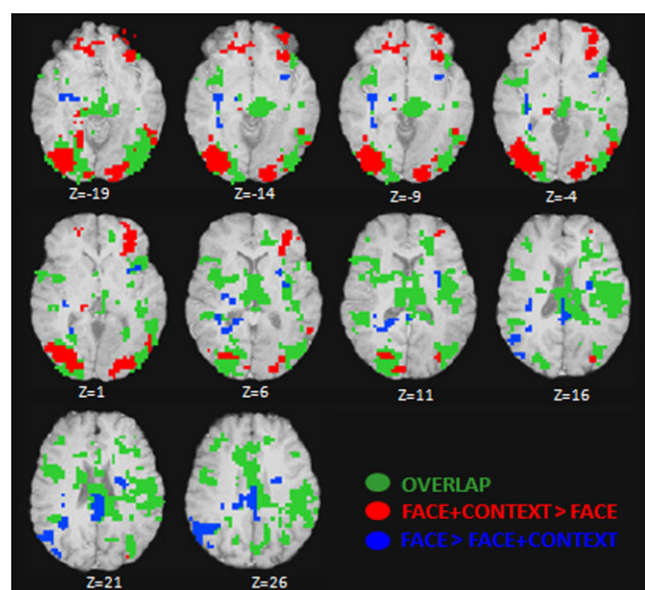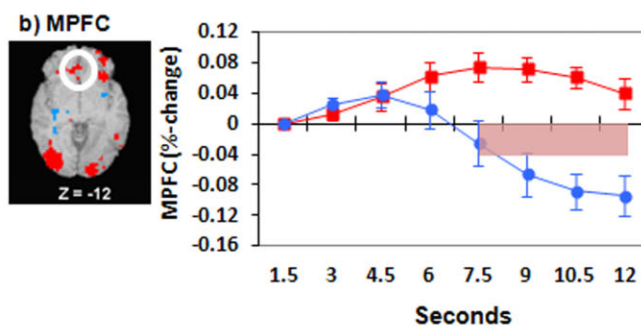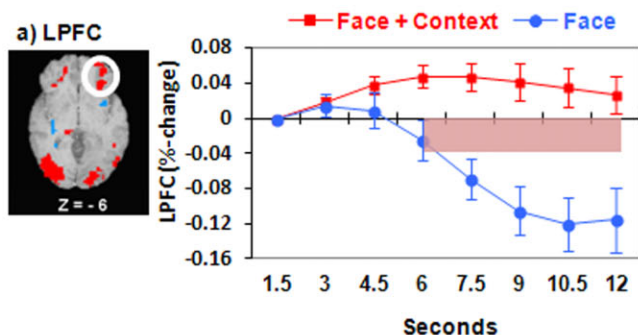
A. FACE+CONTEXT > FACE
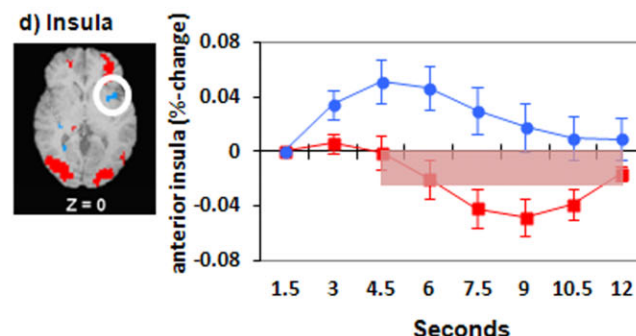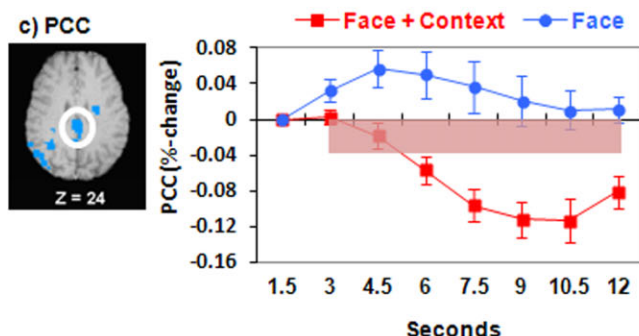

B. FACE > FACE+CONTEXT

Figure 3. A: FACE+CONTENT > FACE. LPFC (a), MPFC (b). B: FACE > FACE+CONTENT. PCC (c), Insula (d). *Note*. Significant differences in time courses between "Face + Context" and "Face" stimuli are highlighted below the *x* axis, pink = $p < .05$.

Activity associated with interactions of context and valence. Context × Valence × Time interactions were observed in several brain areas associated with emotional processing including the VMPFC/rostral ACC (rACC) (BA10/32), VLPFC (BA47), ACC, amygdala, hippocampus, and parahippocampal gyrus ($p < .005$, 24 voxels contiguity; Table 2). Modulation of emotional valence on context effect occurred in prefrontal regions such as the VMPFC. For negative pictures, VMPFC/rACC (BA10/32) yielded significantly more enhanced and sustained responses for faces augmented with contextual information than for faces presented alone (6–12 s: $F(1,10) = 5.94$, $p < .05$, $\eta^2 = .37$) (Figure 5a). However, for positive pictures, there was no significant difference in activity between faces augmented with contextual information and faces presented alone ($p > .90$) (Figure 5a). Modulation of emotional valence on context effect was driven by faces alone in subcortical-limbic regions including the amygdala and parahippocampal gyrus. For negative pictures, the left amygdala extending to the parahippocampal gyrus showed early increased responses to faces presented alone compared to faces with contextual information (3–4.5 s: $F(1,10) = 7.56$, $p < .05$, $\eta^2 = .43$) (Figure 5b). For positive pictures, the left amygdala displayed late increased reactivity to faces presented alone compared to faces with contextual information (10.5–12 s: $F(1,10) = 7.70$, $p < .05$, $\eta^2 = .44$) (Figure 5b).

Sensitivity Analyses

Threshold for discrimination for FACE+CONTEXT and FACE results. Our sample size is quite small, so we performed sensitivity analyses to examine whether our results are robust even in a small sample by showing that nearly every participant conformed to expectations using grid search for optimal prediction of FACE+CONTEXT or FACE given the functional regions of interest (ROIs) (shown in Figures 3–5), as in Siegle et al. (2012). Discrimination between FACE+CONTEXT and FACE was consistent across participants in our functional ROIs except the amygdala (which was relatively consistent across participants; detailed in online S-V). In nearly every functional ROI, optimally predictive thresholds were near 0, so the primary distinctions between FACE+CONTEXT and FACE were whether the ROI activated or de-activated yielding qualitative distinctions between the conditions. Thus, overall, our results were robust even in a small sample.

Anatomical amygdala ROI analysis. An anatomical ROI analysis revealed that the right amygdala appears similarly engaged in processing of both emotional faces alone and emotional faces augmented by contextual information, whereas the left amygdala is neither similarly nor differently involved in processing emotional information conveyed by emotional faces augmented by contextual information and faces alone (see S-VI).

Discussion

We compared subjective emotional experiences and brain networks activated by contextually rich pictures depicting emotional faces to pictures of the same emotional faces presented alone. The goal was to begin to quantify the extent to which lab studies of disembodied nonfamiliar emotional faces miss critical features of real-world information. Consistent with previous studies (e.g., Britton et al., 2006; Geday et al., 2003) and our expectations, faces augmented
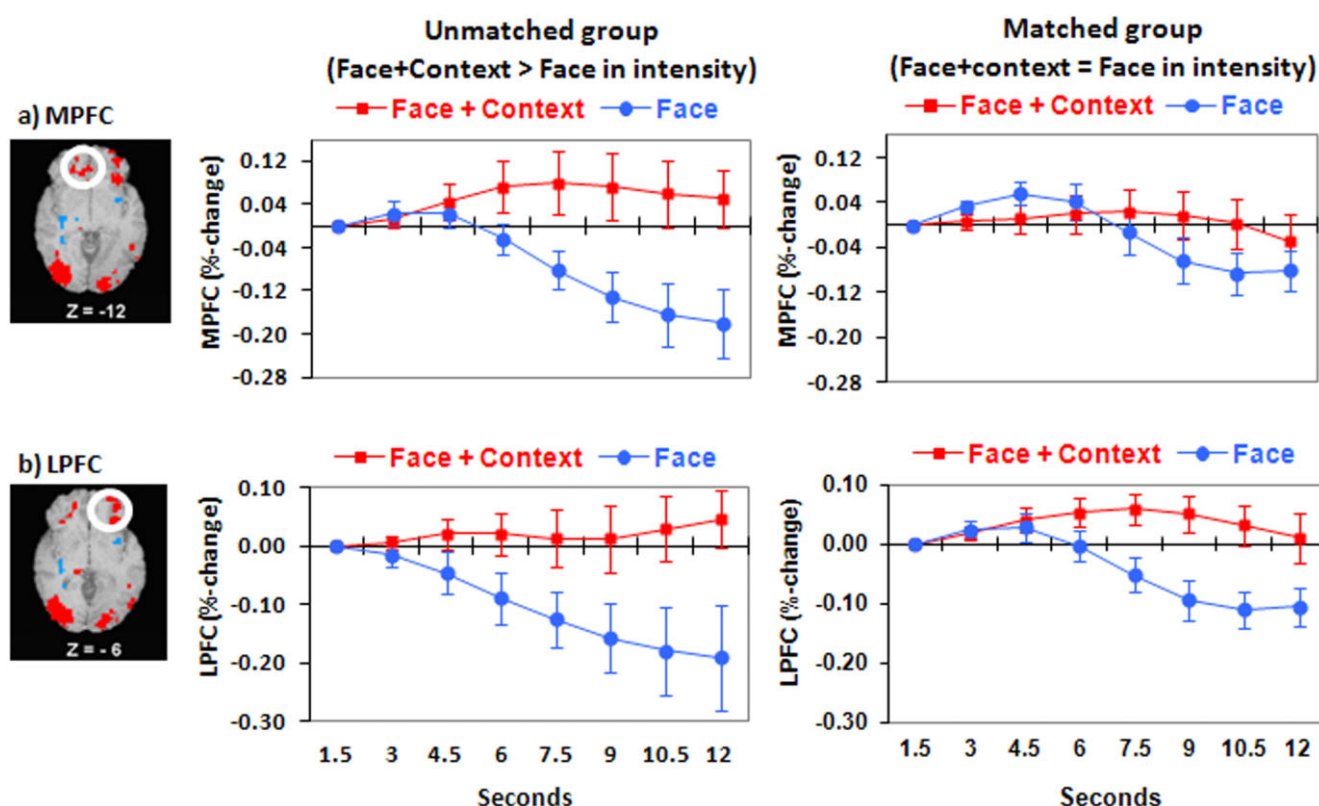
Figure 4. Context × Intensity interaction effect: MPFC (a), Context main effect: LPFC (b). *Note.* Although there were no significant time interaction effects, time courses were plotted to show hemodynamic responses in these regions and temporal dynamics of brain activity were not examined.

by contextual information had many features consistent with ecological validity; they were rated as more affectively intense than faces presented alone, they recruited visual and prefrontal regions more broadly, and these prefrontal region activations varied with subjective emotional intensity. In contrast, faces alone had features consistent with utility as a limited neural if not ecological probe; they were better activators of limbic and paralimbic regions. Both types of stimuli preserved activity expected for general social and emotional processing (e.g., STG and insula) and visual task-related stimuli (e.g., visual processing regions).

Emotional Face Processing

Due to their almost cartoonlike simplicity, emotional faces may represent excellent probes of neural features subserving automatic emotional processing. Compared to faces in context, they more strongly activated limbic/paralimbic regions such as the insula and PCC, previously associated with emotional face processing (e.g., Moriguchi et al., 2005; Phillips et al., 1998). Other areas more strongly associated with faces (e.g., pSTG and precuneus) are involved in emotional and social processing of faces and social

Table 2. *Regions With Significant Interactions of Context × Valence × Time*[a]

Region	BA	Size	Max F	Talairach coordinate			Activation pattern	
				x	y	z	Negative	Positive
Anterior cingulate gyrus	10/32	62	4.07	13	40	9	FC > F	FC = F
Medial frontal gyrus	10	626	8.19	12	51	3	FC > F	FC = F
Inferior frontal gyrus	47/11	616	6.72	28	25	−9	FC < F	FC > F
Supramarginal gyrus	40	351	5.56	53	−50	33	FC < F	FC > F
Inferior occipital gyrus	18	180	5.16	−39	−86	−13	FC > F	FC = F
Inferior occipital gyrus	18	578	6.5	41	−86	−11	FC > F	FC = F
Middle occipital gyrus	19/18	2342	12.17	−38	−83	5	FC > F	FC = F
Parahippocampal gyrus	28	146	6.18	31	−7	−24	FC > F	FC = F
Parahippocampal gyrus	19	469	13.08	−23	−53	−5	FC > F	FC = F
Amygdala		118	6.03	−27	−6	−15	FC < F	FC > F
Cerebellar tonsil		2995	6.84	28	−54	−36	FC > F	FC = F
Inferior semilunar lobule		1030	6.72	37	−69	−40	FC > F	FC = F
Cerebellar tonsil		3884	11.06	−29	−45	−36	FC > F	FC = F

Note. BA = Brodmann area; Size = number of voxels; Max F = maximum F value; FC: FACE+CONTEXT; F: FACE.
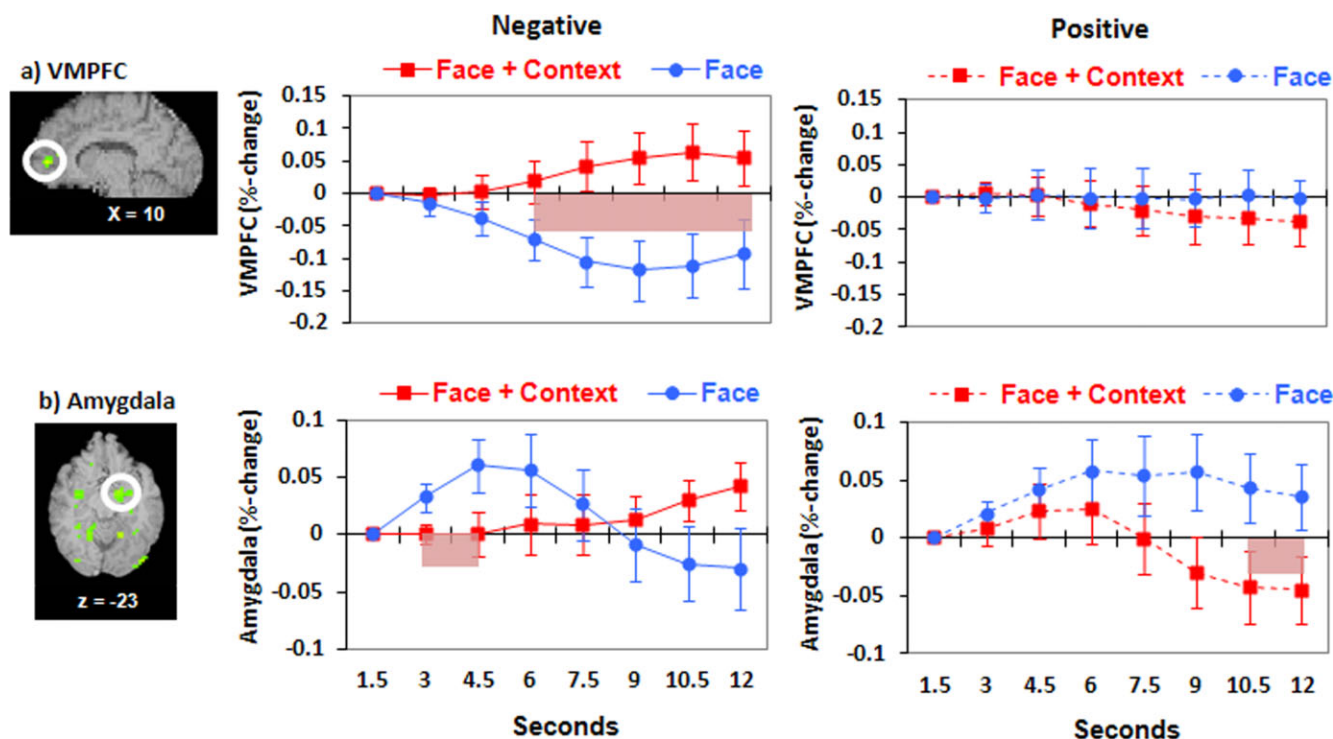[a]$p < .005$, 24 voxels contiguity.

Figure 5. Context × Valence × Time interaction effects: VMPFC (a), Amygdala (b). *Note*. Significant differences in time courses between "Face + Context" and "Face" stimuli are highlighted below the *x* axis, pink = $p < .05$.

behaviors (Adolphs, 2003; Allison, Puce, & McCarthy, 2000; Haxby, Hoffman, & Gobbini, 2002) as well as the processing of other people's mental state (Cavanna & Trimble, 2006; Frith & Frith, 2006; Lee & Siegle, 2012) consistent with ability to devote resources to only social processing of faces. Increased activity in response to emotional faces presented alone in these regions may reflect social processing of faces (e.g., thinking about the person's emotions).

In line with theoretical accounts of emotional face processing (Ekman, 1999; LeDoux, 1996), our finding suggests that emotional processing of faces relies on brain regions associated with relatively quick, automatic emotional processing. The time course of brain activity observed in this study may also support early and automatic processing of emotional faces. For example, the hemodynamic response to faces rose rapidly to a peak (around 4.5 s after the onset of emotional faces). In support of this idea, subcortical-limbic regions such as the left amygdala extending to the parahippocampal gyrus showed particularly robust early neural responses to negative faces compared to negative faces with contexts (for a review, see Fusar-Poli et al., 2009). This result suggests that rapid and automatic emotional processing may be more salient in negative situations compared to positive situations, possibly because automatic responses to negative faces could help avoid threats that are not yet present (e.g., if someone is scared because they know a bear is coming).

Towards Ecological Validity: Increasing Emotional Elaboration and Complexity

As hypothesized, faces augmented with contextual information displayed many features consistent with greater ecological validity. We suggest that there were two features underlying these differences involving increased emotional elaboration and processing of increased complexity. Recruitment of a wide array of prefrontal regions is consistent with increased emotional elaboration and cognitive appraisal of our complex social stimuli (e.g., Cunningham, Johnson, Gatenby, Gore, & Banaji, 2003; Grimm et al., 2006; Hariri, Bookheimer, & Mazziotta, 2000) via cortical pathways for emotional information processing (Clore and Ortony, 2000; Lazarus, 1991). Hemodynamic responses to faces with contextual information in these regions rose slowly to a peak (around 7.5 s after the onset of emotional faces with context) and were sustained during the subsequent fixation, suggesting a potential index of sustained emotional processing associated with contextual information.

Subjective emotional intensity modulated neural responses, for example, in the MPFC, which is involved in subjective emotional experience (e.g., Herbert, Herbert, & Pauli, 2011; Terasawa, Fukushima, & Umeda, 2011), self-relevant processing (e.g., Moran, Macrae, Heatherton, Wyland, & Kelley, 2006; Northoff et al., 2006), and social cognitive processing (e.g., Leopold et al., 2012; Sebastian et al., 2012). Thus, contextual information may allow people to link their own personal experience to emotional stimuli, consequently leading to increased subjective emotional experience. Alternatively, augmented contextual information may help people to more deeply understand other people's emotions displayed by faces and then to feel their subjective emotional responses. Emotional valence also modulated context effects in prefrontal regions. The VMPFC/rACC showed greater and more sustained activity to negative than positive stimuli, potentially consistent with more effortful appraisal in negative situations, which often require action and response, compared to positive situations.

Second, other prefrontal areas may have been more strongly associated with processing of additional complexity of the ecological stimuli (e.g., Gennari, MacDonald, Postle, & Seidenberg, 2007;

Sato et al., 1999). For example, LPFC regions, known to be involved in cognitive or elaborative processing (Badre & Wagner, 2007; Bahlmann, Korb, Gratton, & Friederici, 2012; Raposo, Han, & Dobbins, 2009), were more activated by emotional faces presented with contextual information than emotional faces presented alone. These regions were not affected by subjective emotional intensity.

Limitations and Conclusions

This study had several limitations. Foremost, we did not use neutral control stimuli as they would not have helped to answer questions regarding modulation of subjective emotional experience by ecological stimuli; that said, observed effects could have occurred in neutral faces or scenes without faces if they were due solely, for example, to low-frequency visual features or complexity. This makes specific roles of prefrontal and visual regions in emotional and visual (e.g., context and content) processing hard to disambiguate without further research including well-defined control stimuli. As neutral stimuli are not located at the center of the space defined by valence and arousal continua (e.g., Shah & Lewis, 2003;

Tottenham et al., 2013), these will be subtle effects to tease out. Use of a passive viewing task prevented us from directly examining how specific semantic and other cognitive processing influenced our findings. Finally, we urge caution in generalizing from this study given our relatively small sample size, though we are encouraged by the relative uniformity of results across participants.

These limitations notwithstanding, our findings of enhanced subjective and prefrontal neural response to emotional faces with contextual information suggest that people may feel subjective emotional experience and keep interpreting emotional information conveyed through both faces and contextual information during social interactions. Our study may also have practical implications for future emotion research. For studies in which the only goals are to observe activity associated with relatively quick, automatic processing of emotion and social processing of faces, simple faces may represent excellent stimuli. For studies in which a more holistic view of reactivity to emotional stimuli is desired, or for which brain activity associated with subjective emotional responses is a goal, contextual augmentation may achieve activation throughout brain networks associated with emotional, social, cognitive, and visual processing.

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Supporting Information

Additional supporting information may be found in the online version of this article:

S-I: Information about basic emotions (as a proxy of facial expressions) rated by specific emotion ratings.

S-II. Context effects qualified by arousal ratings.

S-III. Method: Type I error control using "temporal contiguity threshold."

S-IV. Overlapping areas commonly activated by FACE+ CONTEXT and FACE pictures.

S-V. Sensitivity analysis: Threshold for discrimination for FACE+CONTEXT and FACE results.

S-VI. Sensitivity analysis: Anatomical amygdala ROI analysis.

Table S1. Overlapping regions associated with both FACE+ CONTEXT and FACE stimuli.

Figure S1. Discrimination for FACE+CONTEXT and FACE in the functional ROIs (Context × Time).

Figure S2. Discrimination for FACE+CONTEXT and FACE in the functional ROIs (Context × Intensity).

Figure S3. Discrimination for FACE+CONTEXT and FACE in the functional ROIs (Context × Time × Valence).

Figure S4. ROI analysis using anatomically defined amygdala ROI.