Self-Relevance Processing in the Human Amygdala: Gaze Direction, Facial Expression, and Emotion Intensity

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How the processing of emotional expression is influenced by perceived gaze remains a debated issue. Discrepancies between previous results may stem from differences in the nature of stimuli and task characteristics. Here we used a highly controlled set of computer-generated animated faces combining dynamic emotional expressions with varying intensity, and gaze shifts either directed at or averted from the observer. We predicted that perceived self-relevance of fearful faces would be higher with averted gaze—signaling a nearby danger; whereas conversely, direct gaze would be more relevant for angry faces—signaling aggressiveness. This interaction pattern was observed behaviorally for emotion intensity ratings, and neurally for functional magnetic resonance imaging activation in amygdala, as well as fusiform and medial prefrontal cortices, but only for mild- and not high-intensity expressions. These results support an involvement of human amygdala in the appraisal of self-relevance and reveal a crucial role of expression intensity in emotion and gaze interactions.

Because facial expressions convey rich information concerning the state of mind of others (Smith, Cottrell, Gosselin, & Schyns, 2005), some theorists have argued that neuromotor programs of facial expression patterns might serve as the building blocks of emotion communication. Accordingly, Ekman and colleagues have compiled a detailed "alphabet" of facial patterns in which each basic emotion is associated with prototypical facial expressions (Ekman & Friesen, 1978). In turn, for perception, decoding facial expression would also reflect the discrete nature of these facial patterns, each one denoting a specific affective state of the expresser. However, the psychological processes and neural systems responsible for expression recognition still remain debated (Adolphs, 2002; Haxby, Hoffman, & Gobbini, 2000).

In this theoretical framework, gaze direction or gaze shifts have not been considered as a differentiating feature of any prototypical

facial expression. By contrast, other theories based on appraisal processes have explicitly taken into account the influence of gaze on emotion recognition (Sander, Grafman, & Zalla, 2003; Sander, Grandjean, Kaiser, Wehrle, & Scherer, 2007) and argued that decoding facial expression implies a more global appraisal from all observable cues of mental states in the face (Scherer & Ellgring, 2007), among which, for instance, gaze direction represents a critical cue for inferring the focus of attention (Langton, Watt, & Bruce, 2000; Sander et al., 2007). Therefore, contrary to discrete-emotion models, the appraisal theory predicts an influence of gaze direction on the emotion perceived in a face. It is important that this approach to emotion perception does not only suggest that facial cues are decoded as a function of the underlying appraisal processes in the expresser, but also suggests that facial cues are appraised by the observer with respect to their relevance for his or her own needs, goals, values, or well-being (Sander et al., 2007). In this context, the integration of gaze cues and other facial movements should be particularly sensitive to the degree of self-relevance of the perceived expression (Sander et al., 2003): for instance, the aversive dimension of an angry face should increase when one is the object of anger and is gazed at. On the contrary, the self-relevance of threat signaled by a fearful face should increase when this face is looking at something away from the observer (see Manstead & Fischer, 2001).

A previous behavioral study by Sander et al. (2007) directly tested the different predictions from discrete-emotion versus appraisal theories, and demonstrated that judgments of emotional intensity in facial expressions is modulated by concomitant gaze direction, with opposite effects for fear and anger. These data support a role for appraisal of self-relevance in the decoding of facial expression (see also Adams & Kleck, 2003 for consistent behavioral results).

Here we used functional brain imaging to provide further neurophysiological evidence in support of this view. If gaze is an important cue for processing emotional expressions, as predicted by appraisal theories, we should expect that the neural network

activated by facial expressions would show differential responses as a function of the concomitant eye direction. In particular, such effects might be found for the amygdala, a brain structure that may be critical for relevance detection (Sander et al., 2003), and hence exhibit a similar pattern of interaction between gaze and expression as found behaviorally (Sander et al., 2007). Conversely, if gaze does not represent an important perceptual cue for decoding of facial emotions, regions activated by specific expressions (including the amygdala) should respond similarly to a given expression independent of eye direction. Moreover, several neuroimaging studies have shown that the amygdala is involved in processing both eye gaze (e.g., George, Driver, & Dolan, 2001) and emotional expression (Sprengelmeyer, Rausch, Eysel, & Przuntek, 1998; Vuilleumier, Armony, Driver, & Dolan, 2001), making it a plausible site for an integration of these two types of facial cues. In nonhuman primates, the amygdala also contains neurons that are highly sensitive to facial and gaze features (Hoffman, Gothard, Schmid, & Logothetis, 2007). Moreover, bilateral amygdala lesions in humans may produce severe deficits in processing social information from faces, especially for the eye region (Adolphs et al., 2005). Other findings indicate that neurons in temporal cortex may also process both facial features and gaze direction (Perrett et al., 1985), in line with human neuroimaging data showing that superior temporal sulcus (STS) is activated by changes in gaze orientation (averted vs. direct [Allison, Puce, & McCarthy, 2000] or left vs. right [Calder et al., 2007]) as well as by emotional facial expression (Haxby et al., 2000; Vuilleumier et al., 2001). These anatomical overlaps are consistent with important functional interactions between gaze and expression, and raise the possibility that these may take place at multiple sites including the amygdala and temporal cortex.

Three previous neuroimaging studies have investigated the effect of gaze orientation on the brain response to facial expressions (Adams, Gordon, Baird, Ambady, & Kleck, 2003; Hadjikhani, Hoge, Snyder, & de Gelder, 2008; Sato, Yoshikawa, Kochiyama, & Matsumura, 2004) but used different experimental manipulation and produced conflicting results. Sato et al. (Sato, Yoshikawa, et al., 2004) found higher amygdala to angry faces looking toward the participants rather than away from them, consistent with the self-relevance appraisal hypothesis; but this study used only oblique views of faces gazing straight ahead, which does not allow a reliable manipulation of perceived gaze direction (Todorovic, 2006). By contrast, Adams et al. used front-views of emotional faces that were edited to manipulate gaze direction (Adams et al., 2003; Adams & Kleck, 2005), but reported that amygdala activation to angry faces was stronger with averted than direct gaze, but conversely stronger to fearful faces with direct than averted gaze. Hadjikhani et al. (2008) also used front-views of emotional faces that were also edited to manipulate gaze direction but, contrary to Adams et al. (2003), Hadjikhani and her colleagues (2008) observed stronger amygdala activation to fearful faces with averted than direct gaze. Beside differences in expression and gaze manipulation, a limitation common to previous imaging and behavioral studies is that static facial displays were used, which may undermine their ecological validity since both gaze and expression phenomena are dynamic in nature. For instance, clear distinctions have been shown between effects of gaze direction and gaze shift (Conty, N'Diaye, Tijus, & George, 2007). Furthermore, relative to static displays, dynamic stimuli can enhance amygdala response (La-

Bar, Crupain, Voyvodic, & McCarthy, 2003; Sato, Kochiyama, Yoshikawa, Naito, & Matsumura, 2004) and intensity judgments (Biele & Grabowska, 2006) to emotional faces.

In the present study, we therefore used dynamic rather than static stimuli. In addition, we also manipulated the intensity of expression since previous studies using morphs between neutral and expressive faces (e.g., Glascher, Tuscher, Weiller, & Buchel, 2004) or testing subjective judgments (Kim, Somerville, Johnstone, Alexander, & Whalen, 2003) have reported that amygdala activation correlates positively with the perceived intensity of emotion. To this aim, we employed a highly controlled stimulus set with computer-generated faces animated according to a realistic three-dimensional (3D) model, allowing a precise control of eye motion and facial muscle movements, both in terms of time-course and intensity. We predicted that the amygdala should show selective modulations depending on eye gaze direction, with angry faces producing greater responses with a direct than averted gaze, but fearful faces conversely producing greater responses with averted than direct gaze (Sander et al., 2003).

Method

Participants

Twenty-four healthy participants were recruited, all right-handed, with normal or corrected-to-normal visual acuity, and free of history of psychiatric or neurological illness, or drug or alcohol abuse. All participants gave informed consent in agreement with the local ethical committee regulation. Because of technical problems, data from 2 participants were discarded, leaving 22 participants in the final group (12 women; mean age: 25.9).

Stimuli and Task

We designed a new stimulus set using a computer-graphics methodology based on 3D face-modeling tools, allowing fine variations of gaze direction and a large spectrum of emotional expressions varying in intensity. This was implemented through FACSGen, a software currently developed in our center (Roesch, Reveret, Grandjean, & Sander, 2006) as an extension to FaceGen Modeler 2.0 (Singular Inversion Inc. http://www.FaceGen.com). FACSGen uses the 3D face-rendering processor of FaceGen, but is designed to manipulate expressions in 3D faces with a strict temporal control of their animation and independent muscle parameters derived from the Facial Action Coding System (Ekman & Friesen, 1978). The FaceGen software provides a library of routines to control morphology, as well as expression of realistic face avatars in a parametric manner, which enabled us to produce intermediate faces that are not based on morphing but generated from the anatomical configuration of individual facial action units. Gaze deviation was created by angular rotation of the eye, relative to the axis of the head, via computation of the displacement of the iris texture on a spherical surface that modeled the eyeball. In the present study, we used gaze deviations to either side (left/right) to generate the different gaze shift conditions. In addition, we manipulated facial action units corresponding to three emotion types (fear, anger, happy) and two emotion intensities (mild vs. intense), yielding six expressions, plus a neutral condition (see Figure 1). Although we did not have specific a priori hypotheses regarding

Figure 1. Combination of facial expression and gaze shift in animated faces. Illustration of the stimulus categories used in our study. Realistic faces were created with FACSGen software, allowing a parametric manipulation of individual facial action units, intensity, and gaze direction. From left to right: neutral expression with (leftward) averted gaze; intense angry expression with direct gaze for the same male identity; mild fear expression with (leftward) averted gaze in a female face; and intense happy expression with (rightward) averted gaze in another male face. Heads were cropped to exclude any paraphernalia, such as hair.

happy expressions, these were included with the aim to counterbalance the negative expressions of anger and fear, making them possibly more relevant, and to reduce the possibility of habituation or expectation effects in participants who had to repeatedly rate the expressions throughout the experiment. Mild-intensity expressions were obtained by using only the half of the displacement of meshes modeling the full expressions, but we kept the speed of the animation constant so that the mild expressions unfolded over a half-time window (see below).

All expressions and gaze shift conditions were combined in different face identities to produce movie clips of 3 to 4 s in duration. On each trial, following a fixation cross (250 ms), a neutral face gazing either toward or away from the subject was presented. After a variable delay (2–3 s), a gaze shift was initiated by a 100-ms movement of both eyes, either from straight to averted (leftward or rightward), or from averted to straight (direct eye contact). After another 100-ms delay, emotional expression unfolded from a neutral to mild (50%) or high (100%) intensity over a period of 200 or 400 ms, respectively, and was then maintained for another 400 or 200 ms, respectively. The rise time of low-intensity expressions was therefore always 200-ms long, whereas the rise-time of high-intensity expressions was always 400 ms. A static face display was maintained on screen up to a total stimulus duration of 2 to 3 s, to compensate for these differences in the unfolding of expressions, so that the two conditions of mild- and full-intensity expressions were actually matched with respect to the global duration of the face display (the dynamic unfolding of low-intensity expressions was followed by a 400-ms static display with the 50% expression, high-intensity expressions were displayed by a static face for another 200 ms after the 400-ms rise time). The face was then

replaced by the response screen bearing the word "intensity" for 2 s, during which participants gave their rating. A blank screen was then displayed during the 500-ms intertrial interval.

Variable durations were chosen for the initial static phase, as well as for the subsequent expression-plus-gaze changes, to avoid any predictability or expectancy due to regular presentation, and to jitter onset times during functional magnetic resonance imaging (fMRI) for uniform sampling of hemodynamic responses. Sixteen different identities were generated, and each identity was animated using the same set of parameters, leading to a fully crossed design of gaze and expression within each identity (see Table 1). These conditions were shown in an intermingled pseudorandom order, and repeated in four blocks of 9 min each.

During fMRI, participants were instructed to look at the faces and to rate the emotional intensity of their expression on a 4-point Likert scale (no emotion/low/moderately high/very high emotion), by pressing one of four buttons with their right hand. Stimulus presentation and response acquisition were controlled through E-Prime 2.0 (Psychology Software Tools Inc., Pittsburgh).

Image Acquisition and Data Processing

Imaging data were collected on a 3T Trio Siemens scanner at Geneva Hospital (Center for Bio-Medical Imaging), using standard functional MRI parameters: EPI T2* sequences, TE: 30 ms, TR: 2.2 s, Flip Angle: 85°, 40 slices of 3-mm thickness with whole brain coverage, FOV: 240 mm, in-plane resolution of 3 by 3 mm. Functional activation was measured through 240 EPI volumes for each of the four runs of 9 min in duration (excluding 5 initial volumes to allow for T1 equilibration). Coronal T1-weighted structural images were obtained for each subject using standard MPRAGE sequence (TR: 2.2 s; TE: 2.89 ms; TI: 1 s).

Functional images were preprocessed and analyzed using the general linear model for event-related designs in SPM2 (Wellcome Dept. of Imaging Neuroscience, London, U.K.; http://www.fil.ion.ucl.ac.uk/spm). EPI volumes were realigned, corrected for slice timing, normalized to an EPI template (resampled voxel-size of 3 mm), and spatially smoothed (8-mm FWHM Gaussian kernel). Hemodynamic response functions were estimated separately for the onset of the baseline face (static), the onset of the gaze shift with concomitant emotional expression (for each intensity), and the motor response. Correlations between the face onset regressors and the regressors modeling facial movements (combination of gaze and expression) were low, all below 0.35. We also included six motion-correction parameters extracted from the realignment procedure. A high-pass frequency filter (cutoff 128 s) and first-

Table 1

Distribution of Conditions and Stimuli

| Gaze direction | | Emotional expression: type and intensity | | | | | | |
| | | | Fearful | | Angry | | Happy | |
Initial	Final	Neutral	Mild	Intense	Mild	Intense	Mild	Intense
Direct	Averted Left	16	8	8	8	8	8	8
	Averted Right	16	8	8	8	8	8	8
Averted Left	Direct	16	8	8	8	8	8	8
Averted Right		16	8	8	8	8	8	8

order auto-regressive corrections for auto-correlation between scans were applied. For each contrast of interest, images of parameter estimates were computed for individual participants, and then entered into a second-level group analysis using a one-sample t test. To assess the significance of random effects, we used an uncorrected $p < .005$ voxel-wise threshold, that is, T = 2.831 with 21 degrees of freedom, with a minimal cluster size of 20 voxels. Individual structural images were also normalized to a standard template in the Montreal Neurological Institute (MNI) coordinate space and averaged to produce a mean anatomical image on which to project activation sites. Coordinates are given in millimeters in MNI space.

Statistical analyses of behavioral results were also conducted under Matlab. For all repeated-measures analyses of variance (ANOVA), the alpha level of significance was .05, Huynh-Feldt corrected if appropriate.

Results

Behavioral Results

Subjective ratings of emotion intensity by the participants were reliably modulated by the nature of the expression, its intensity, and direction of gaze (see Figure 2). A two-way repeated-measure ANOVA using the factors Expression (Neutral-Fearful-Angry-Happy) × Gaze shift (Direct-Averted) showed a main effect of expression, $F(3, 63) = 138.7; p < .001$, and an interaction between expression and gaze, $F(3, 63) = 9.82; p < .001$, but no main effect of gaze, $F(1, 21) = 2.9; p > .1$. To further investigate this interaction and the role of intensity for the emotional faces, we then run a three-way repeated-measure ANOVA with factors Emotion (Fearful-Angry-Happy), Gaze (Direct-Averted), and Intensity (Mild-Intense). Because the neutral condition cannot be decomposed into low- versus high-intensity conditions, we then excluded the Neutral condition from the following factorial analyses. Note that to make this unambiguous, we used a different name for the first factor of these ANOVAs, with the label EXPRESSION referring to the factor manipulating facial emotions on four levels (Fearful, Angry, Happy and Neutral), but the label EMOTION referring to the three levels differentiating emotional faces only (that is, excluding the Neutral condition). This second analysis showed that the main effects of Emotion, $F(2, 42) = 49.41; p < .001$, and Intensity, $F(1, 21) = 158.7; p < .001$, were significant, but not Gaze, $F(1, 21) = 1.7; p > .1$. Critically, the triple interaction between these factors, $F(2, 42) = 17.31; p < .001$, and the double interaction Emotion × Gaze, $F(2, 42) = 13.7; p < .001$, were

significant. Other interaction terms were not ($F < 3$). As our hypothesis was primarily based on the modulation of fear and anger emotion judgment by gazes, we then focused on these two emotions. One can note, however, that the ratings of happiness were also modulated by gaze but for high-intensity displays only (higher ratings with direct than averted gaze; T = 4.03, $p < .001$).

The gaze-by-emotion interaction pattern was still significant when we focused on the two main emotions of interest in this study: the triple interaction (Fear-Anger) × (Mild-Intense) × (Direct-Averted) was significant, $F(1, 21) = 21.7; p < .001$, and indicated that the effect of gaze on expression perception differed according to expression intensity. Further, Emotion and Gaze interacted, $F(1, 21) = 82.9$ for mild-intensity displays but not for high-intensity displays, $F(1, 21) = 0.1$. Post hoc one-tailed test of simple effects confirmed that mild (50%) angry expressions were judged as more intense with direct than averted gaze, T(21) = 6.45; $p < .001$, while gaze had a reverse effect for mild fearful expressions (T[21] = −2.18; $p < .05$). By contrast, ratings of high-intensity fearful (T[21] = 1.68; $p > .1$) and angry (T[21] = −1.60; $p > .1$) expressions did not vary with gaze.

fMRI Results

Main effect of emotion. We first identified emotion-responsive regions by contrasting all expressive faces (Fear, Anger, and Happiness) to Neutral faces. This showed activation in ventral occipito-temporal cortex bilaterally (see Figure 3), including face-sensitive regions in fusiform cortex that exhibited increases for each emotion relative to neutral (all $p < .001$, Figure 4b). In addition, bilateral amygdala also showed significant increases to emotional faces (see Figure 3), as well as the paracingulate/medial prefrontal cortex (MPFC), left inferior frontal cortex, left parietal cortex, and central sulcus (see Table 2). This set of areas activated by emotional expressions was then used (with a lenient threshold of $p < .01$) to define a mask of regions of interest (ROIs), allowing us to constrain our subsequent analyses of modulation by gaze and intensity to emotion-sensitive voxels.

To determine the effect of emotion intensity, we contrasted the two degrees of expression intensity (intense vs. mild) across all emotions within the ROI mask defined above. This revealed increases in the right middle occipital gyrus (−51 −66 0, T = 3.36) and bilateral fusiform (−18 −60 −15, T = 3.85 and +24 −69 −12, T = 3.42), as well as a similar trend in the left amygdala (T = 2.37), indicating that these areas activated by emotional faces were also sensitive to expression intensity.

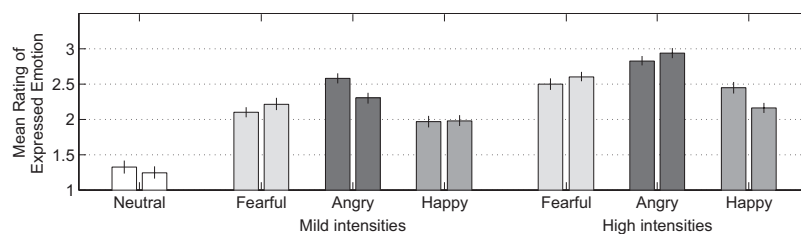*Figure 2.* Ratings of perceived intensity for the different face conditions. Participants rated the expressed emotion on a 4-point scale (from none to highly intense). For each expression, the left bar represents faces with gaze shifts from averted to direct; and the right bar represents faces with the inverse gaze shift from direct to averted. Error bars indicate the repeated-measures standard error around the mean.
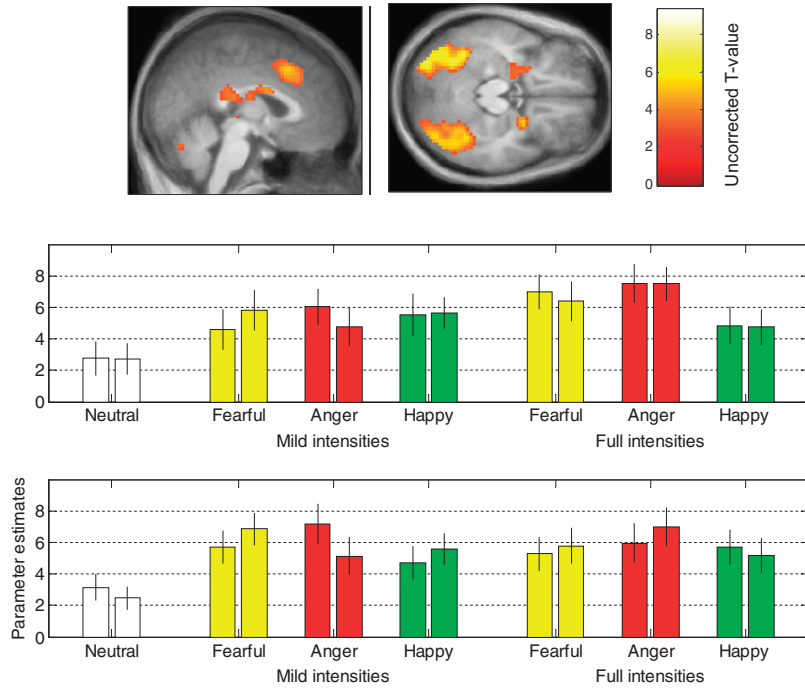
Figure 3. Main effect of emotional versus neutral expressions. *Top*: Brain regions showing increased response to all emotional facial expressions (Fearful + Angry + Happy) relative to Neutral faces ($p < .005$ uncorrected), including bilateral amygdala, fusiform gyri, and medial paracingulate frontal cortex. *Middle & Bottom*: Parameter estimates of activity (in arbitrary units) for the left fusiform and paracingulate regions shown above. For each expression, the left bar represents the response to direct gaze shifts and the right bar represents the response to averted gaze shifts.

Main effect of gaze direction. We examined neural response to changes in gaze direction by contrasting the two types of gaze shift across all expression categories in the whole brain. Both the right and left posterior portions of superior temporal sulcus (pSTS; right: $+45$ $-66 +12$; T = 4.49; and left: $-57 -42 +9$; T = 3.85) as well as the intraparietal sulcus (IPS; $-42 -57 +45$; T = 3.70) were more activated by averted than by direct gaze. It is interesting that this differential responses to gaze shifts arose with all emotional

expressions (all T > 1.72, i.e., $p < .05$), but not with neutral faces (T < 0.86, $p > .2$).

Interaction of gaze and emotion. The key interaction of gaze and expression was tested by comparing high self-relevant expressions (Averted Fear + Direct Anger) versus low self-relevant conditions of the same expressions (Direct Fear + Averted Anger). To constrain this analysis to emotion-sensitive regions, we again used the ROI mask previously defined by the main effect of
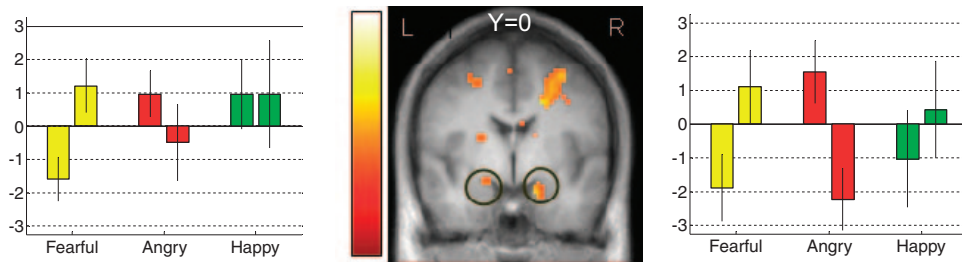

Figure 4. Modulation of amygdala responses to emotion by gaze direction. Parameter estimates of activity (in arbitrary units) for the left and right amygdala clusters showing significant interaction between gaze and mild expressions of fear, anger and happiness. In each graph, the left bar of each pair represents the response to direct gaze shifts and the right bar represents the response to averted gaze shifts. Parameter estimates were mean-corrected relatively to the baseline activity corresponding to average beta value across all conditions. The illustration in the middle shows a coronal slice of the functional interaction ($p < .05$, uncorrected) at the coronal slice y = 0 where both clusters are visible (circled in black). Amygdala activation also extended more ventrally in anterior slices for the right side and more dorsally in posterior slices for the left side.

Table 2
Brain Areas Activated by Emotional Expressions (Fear + Anger + Happy > Neutral)

Region	Side	Peak t-value[*]	MNI coordinates (x y z)
Extrastriate/inferior occipital gyrus	Left	9.31	−30 −90 −6
Extrastriate/inferior occipital gyrus	Right	6.94	+36 −90 −6
Fusiform gyrus	Left	9.03	−33 −66 −18
Fusiform gyrus	Right	6.38	+45 −66 −12
Middle occipital gyrus	Left	5.94	−51 −72 0
Middle occipital gyrus	Right	3.36	+45 −72 −3
Inferior/lateral prefrontal	Left	7.41	−54 +12 +18
Dorsal cingulate/medial prefrontal	Left/bilateral	5.34	−6 +24 +51
Inferior parietal lobe	Left	5.69	−30 −45 +39
Central sulcus	Left	6.17	−36 −24 +57
Amygdala	Right	5.19	+24 +6 −15
Amygdala	Left	4.09	−24 +3 −18

[*] All < .005 voxelwise, cluster size > 20 voxels.

emotion (Fear + Anger + Happy vs. Neutral faces). When high and mild expression intensities were combined, no region was found to show such pattern of responses. However, as our behavioral results indicated a significant interaction of Gaze and Emotion for mild intensities only (see above), a similar analysis was performed using conditions with mild-Fear and mild-Anger alone. This revealed a significant interaction in bilateral inferior occipital gyri (−39 −87 −12, T = 3.69; +36 −84 −15, T = 4.62), right fusiform (+45 −63 −18, T = 4.06), right inferior parietal lobule (+51 −39 +42, T = 4.14), and right middle frontal gyrus (+54 +15 +24; T = 3.95) [see Figure 3]. Critically, this interaction was also found for two clusters in the amygdala, on both the right (+24 +6 −24, T = 2.97) and as a trend on the left side (−21 +3 −12, T = 2.61, p < .05).

Such pattern of interaction was restricted to the mild intensity of emotional expressions. This was confirmed by a repeated-measure ANOVA performed on the average parameter estimates of activity (betas) extracted from both right and left amygdala clusters (centered on the main effect of emotion, i.e., Fear + Anger + Happy > Neutral). This analysis showed a significant triple interaction between Gaze (Direct/Averted), Emotion (Fear/Anger), and Intensity (Mild/High) in the right and left amygdala clusters, respectively, $F(1, 21) = 9.85$, $p < .005$, and $F(1, 21) = 8.58$, $p < .01$. This triple interaction was further qualified as the factor Gaze was significant only for the mild intensity of anger and fear, $F(1, 21) = 8.8$; $p < .01$ and $F(1, 21) = 6.8$; $p < .05$, but not for the high intensity conditions, both $F(1, 21) < 2.5$, $p > .13$. Finally, for happy faces, we observed no effect of gaze in simple contrasts between averted and direct gaze (all $p > .1$). See Figure 4.

Discussion

By systematically manipulating gaze and emotional expression in animated faces, we found a significant interaction between gaze direction and facial expression on the subjective ratings of emotion. Anger was judged as more intense when the facial expression was preceded by a gaze shift toward the observer, as compared with when the same facial expression followed a gaze shift away from the observer. On the contrary, fear was judged more intense when the face gazed away, as compared with when the same

fearful face looked at the observer. However, this interaction critically depended on the intensity of expression such that only mild fear and mild anger were significantly modulated by the direction of gaze, while at full intensity, ratings of these emotional expressions were not affected by gaze direction.

In keeping with these behavioral results, our fMRI data also demonstrated that gaze direction modulated neural responses to fearful and angry expression only when such expressions were of mild intensity, with such interaction pattern observed in several brain regions that were sensitive to emotions, including the amygdala, fusiform cortex, and paracingulate/MPFC.

These data corroborate previous behavioral findings obtained with a different set of dynamic face stimuli (Sander et al., 2007), as well as previous imaging results showing greater amygdala response to fearful faces directed away from rather than toward the observer (Hadjikhani et al., 2008), as well as results showing greater amygdala response to angry faces directed toward rather than away from the observer (Sato, Yoshikawa et al., 2004), although the latter manipulation was obtained with oblique views of faces with straight gaze that were presented at different locations in the visual field (rather than with gaze cues per se, see Todorovic, 2006). In line with our predictions, these new results suggest that the amygdala is involved in processing the subjective emotional relevance and not only intrinsic dimensions of facial features (e.g., emotion categories). Our data provide novel support to this view by using a direct and realistic manipulation of gaze, and demonstrating a differential effect of gaze direction for anger and fearful expressions on amygdala responses. This pattern accords with recent proposals that the human amygdala may constitute an evolved system for appraisal of self-relevance rather than a "fear module" or a system dedicated to the processing of emotional arousal (Sander et al., 2003).

Our results contradict those of Adams et al. (Adams et al., 2003) who reported an interaction of gaze and expression opposite to the pattern found here, that is, greater amygdala responses to pictures of angry faces with averted gaze and to fearful faces with direct gaze. In their discussion, Adams and Kleck (2003) argue that the opposite pattern of interaction between gaze direction and facial expression (namely, stronger responses to averted angry and direct

fearful faces) reflected the involvement of amygdala in the processing of ambiguity related to the conflict in the behavioral tendencies conveyed by approach-related cues (angry face, direct gaze) and avoidance-related ones (fearful face, averted gaze). We fully concur with these authors that ambiguous behavior from the expresser (or conflicting cues) offers a valid explanation for their behavioral (longer reaction times) as well as for their fMRI results which show stronger activation of the amygdala in the conflict conditions. The amygdala has indeed been shown to be sensitive to ambiguous emotional signals (Kim et al., 2003), especially those associated with threat (Whalen, 1998). However, this explanation cannot apply to our own results which demonstrate an opposite interaction pattern: conditions of conflicting cues (i.e., of higher ambiguity) trigger lower responses in the amygdala than condition of congruent cues (i.e., of lower ambiguity). One must acknowledge that a single theory cannot explain the opposite results found by Adams et al. (2003) and us.

Therefore, further research is needed to explain the opposite results reported by Adams et al. (2003), on the one hand, and, those observed by the current study, as well as by Hadjikhani et al. (2008) and Sato et al. (2004), on the other hand. However, a possible explanation for contradictory results between these studies might already be found in the influence of emotion intensity on gaze-related effects, as we observed that the critical self-relevance interaction arose for mild but not intense expressions. It is possible that the interaction found behaviorally by Sander et al. (2007) might have been favored by their use of schematic faces, displaying relatively weak emotions. By contrast, a stimulus set such as that of Ekman & Friesen (1978), used in other studies (Bindemann, 2007), might correspond to intense displays of facial emotions, and thus minimize the influence of gaze direction on the recognition of expression (see Bindemann, 2007). In support of this idea, a recent behavioral study (Graham & LaBar, 2007) showed that gaze direction may interfere with speeded recognition of emotion expression only for intermediate morphs between neutral and prototypical expression, not for faces with full-blown expressions.

Finally, amygdala activation in these different studies might potentially reflect two different types of integration of gaze and expression cues: when using emotional faces with prototypical approach/avoidance signals and averted/direct gaze (as Adams & Kleck, 2003), one could observe amygdala responses due to the appraisal ambiguity of conflicting cues; whereas in our own studies (and possibly, in Sato et al. [2004] and Hadjikhani et al. [2008]), the appraisal of emotional faces would benefit from additional cues provided by gaze direction when expression intensity is weak. Further research using different manipulations of expression, gaze, and intensity is necessary to test whether interaction effects of expression and gaze in the amygdala primarily reflect its role in ambiguity processing or relevance detection. The recent results of Hadjikhani et al. (2008) showing stronger amygdala activation to fearful faces with averted gaze, as compared with direct gaze also speak in favor of a role of the amygdala in relevance detection because, in their stimuli, gaze was displaced laterally and toward the ground as if indicating the presence of a nearby danger on the floor (e.g., a snake), which might thus increase the perceived self-relevance of the face rather than its ambiguity.

Taken together, our results strongly suggest that processing gaze direction does contribute to the perceived emotional relevance of facial expression, both behaviorally and neurally as indexed by amygdala response, but particularly for mild-intensity expression where facial features alone may evoke relatively weak emotion signals.

Beside the amygdala, we also observed a strong effect of emotional expression on several cortical regions, including extrastriate visual areas in occipital and fusiform gyri bilaterally, in accordance with the role of these regions in processing emotional (Vuilleumier et al., 2001) and dynamic features in faces (Sato, Kochiyama et al., 2004). Accordingly, these responses were also modulated by emotion intensity (Surguladze et al., 2003). These emotional increases in visual areas appear consistent with attentional modulations driven by the amygdala response (Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004). Note that although activation in lateral occipital areas may at least partly reflect the different amount of visual motion in animated displays, which varied between emotional and neutral conditions, as well as between high- and low-intensity expressions (as in other studies using animated facial displays [LaBar et al., 2003]), eye-gaze motion was present and similar across all stimulus conditions in our study. Since our interest was focused on the interaction pattern between the nature of emotional expressions and the direction of gaze, this difference in motion information is not critical for our conclusion, as it would imply an unlikely interaction between the amount of facial movement (in fearful and angry expressions) and the pattern of eye movements (which differed only in terms of direction not quantity).

It is interesting that emotional expression also modulated activity in the paracingulate/medial prefrontal cortex, a region thought to be critically involved in socioaffective processing and mentalizing (Frith & Frith, 2006). This pattern may reflect the orientation of attention to self-relevant events (Bush, Luu, & Posner, 2000), as well as the recruitment of cognitive processes necessary to decipher emotions and intentions expressed by others (Conty et al., 2007; Ochsner et al., 2004). It is also possible that specific task demands such as fixation, requiring inhibition of a prepotent gaze-following response (Driver et al., 1999), might contribute to activate these regions in anterior cingulate and medial prefrontal cortices (Brown, Vilis, & Everling, 2008).

Finally, the pSTS showed greater response to averted gaze as compared with direct gaze, although these two conditions were equivalent in terms of motion and visual change. STS is critically involved in a variety of implicit and explicit tasks related to social cognition, including gaze and expression (Conty et al., 2007; Pelphrey & Morris, 2006; Pourtois et al., 2004), as well as body gestures and lip movements (Allison et al., 2000). The direction of this effect in our study (averted > direct gaze) corroborates recent findings (Engell & Haxby, 2007) with neutral faces, although here this activation in STS arose specifically with emotional faces (regardless of expression category) but not neutral faces, suggesting that processes normally recruited to infer particular mental states or intentions might have been more activated in STS when emotional faces were seen with averted rather than direct gaze. In addition, we also found that the right inferior parietal lobule (IPL) showed significant interaction between gaze and emotional expression. This region has been shown to respond to gaze shifts jointly with the STS (Pelphrey & Morris, 2006), and might be involved at a later stage of processing, for example to implement attention shifts according to both the direction and relevance of the gaze cues (Vuilleumier et al., 2001).

To conclude, by using a dedicated set of highly controlled dynamic face stimuli, we provide both behavioral and neuroimaging evidence in support of the appraisal of self-relevance in emotion perception, and propose a critical role for the amygdala in such appraisal. In contrast to classic assumptions of basic emotion theories, we show that perceived anger and fear in faces is influenced by concomitant shift as in eye gaze, rather than by specific configurations of facial muscles alone, in a way that is consistent with an integration of distinct cues to evaluate the self-relevance of facial signals.

References

Adams, R. B., Gordon, H. L., Baird, A. A., Ambady, N., & Kleck, R. E. (2003). Effects of gaze on amygdala sensitivity to anger and fear faces. *Science, 300,* 1536.

Adams, R. B., & Kleck, R. E. (2003). Perceived gaze direction and the processing of facial displays of emotion. *Psychological Science, 14,* 644–647.

Adams, R. B., & Kleck, R. E. (2005). Effects of direct and averted gaze on the perception of facially communicated emotion. *Emotion, 5,* 3–11.

Adolphs, R. (2002). Neural systems for recognizing emotion. *Current Opinion in Neurobiology, 12,* 169–177.

Adolphs, R., Gosselin, F., Buchanan, T. W., Tranel, D., Schyns, P., & Damasio, A. R. (2005). A mechanism for impaired fear recognition after amygdala damage. *Nature, 433,* 68–72.

Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in Cognitive Sciences, 4,* 267–278.

Biele, C., & Grabowska, A. (2006). Sex differences in perception of emotion intensity in dynamic and static facial expressions. *Experimental Brain Research, 171,* 1–6.

Bindemann, M., Burton, M. A., & Langton, S. (2007). How do eye gaze and facial expression interact? *Visual Cognition, 16,* 708–733.

Brown, M. R., Vilis, T., & Everling, S. (2008). Isolation of saccade inhibition processes: Rapid event-related fMRI of saccades and nogo trials. *Neuroimage, 39,* 793–804.

Bush, G., Luu, P., & Posner, M. I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Sciences, 4,* 215–222.

Calder, A. J., Beaver, J. D., Winston, J. S., Dolan, R. J., Jenkins, R., Eger, E., et al. (2007). Separate coding of different gaze directions in the superior temporal sulcus and inferior parietal lobule. *Current Biology, 17,* 20–25.

Conty, L., N'Diaye, K., Tijus, C., & George, N. (2007). When eye creates the contact! ERP evidence for early dissociation between direct and averted gaze motion processing. *Neuropsychologia, 45,* 3024–3037.

Driver, J., Davis, G., Ricciardelli, P., Kidd, P., Maxwell, E., & Baron-Cohen, S. (1999). Gaze perception triggers reflexive visuospatial orienting. *Visual Cognition, 6,* 509–540.

Ekman, P., & Friesen, W. V. (Eds.). (1978). *Facial action coding system.* Palo Alto CA: Consulting Psychologists Press.

Engell, A. D., & Haxby, J. V. (2007). Facial expression and gaze-direction in human superior temporal sulcus. *Neuropsychologia, 45,* 3234–3241.

Frith, C. D., & Frith, U. (2006). The neural basis of mentalizing. *Neuron, 50,* 531–534.

George, N., Driver, J., & Dolan, R. J. (2001). Seen gaze-direction modulates fusiform activity and its coupling with other brain areas during face processing. *Neuroimage, 13,* 1102–1112.

Glascher, J., Tuscher, O., Weiller, C., & Buchel, C. (2004). Elevated responses to constant facial emotions in different faces in the human amygdala: An fMRI study of facial identity and expression. *BMC Neuroscience, 5,* 45.

Graham, R., & LaBar, K. S. (2007). Garner interference reveals dependencies between emotional expression and gaze in face perception. *Emotion, 7,* 296–313.

Hadjikhani, N., Hoge, R., Snyder, J., & de Gelder, B. (2008). Pointing with the eyes: The role of gaze in communicating danger. *Brain and Cognition, 68,* 1–8.

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences, 4,* 223–233.

Hoffman, K. L., Gothard, K. M., Schmid, M. C., & Logothetis, N. K. (2007). Facial-expression and gaze-selective responses in the monkey amygdala. *Current Biology, 17,* 766–772.

Kim, H., Somerville, L. H., Johnstone, T., Alexander, A. L., & Whalen, P. J. (2003). Inverse amygdala and medial prefrontal cortex responses to surprised faces. *Neuroreport, 14,* 2317–2322.

LaBar, K. S., Crupain, M. J., Voyvodic, J. T., & McCarthy, G. (2003). Dynamic perception of facial affect and identity in the human brain. *Cerebral Cortex, 13,* 1023–1033.

Langton, S. R., Watt, R. J., & Bruce, I. I. (2000). Do the eyes have it? Cues to the direction of social attention. *Trends in Cognitive Sciences, 4,* 50–59.

Manstead, A. S. R., & Fischer, A. H. (2001). Social Appraisal: The social world as object of and influence on appraisal processes. In K. R. Scherer, A. Schorr, & T. Johnstone (Eds.), *Appraisal processes in emotion: Theory, methods, research.* New York: Oxford University Press.

Ochsner, K. N., Knierim, K., Ludlow, D. H., Hanelin, J., Ramachandran, T., Glover, G., et al. (2004). Reflecting upon feelings: An fMRI study of neural systems supporting the attribution of emotion to self and other. *Journal of Cognitive Neuroscience, 16,* 1746–1772.

Pelphrey, K. A., & Morris, J. P. (2006). Brain mechanisms for interpreting the actions of others from biological-motion cues. *Current Directions in Psychological Science, 15,* 136–140.

Perrett, D. I., Smith, P. A., Potter, D. D., Mistlin, A. J., Head, A. S., Milner, A. D., et al. (1985). Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proceedings of the Royal Society of London Series B, Containing papers of a Biological character Royal Society (Great Britain), 223,* 293–317.

Pourtois, G., Sander, D., Andres, M., Grandjean, D., Reveret, L., Olivier, E., et al. (2004). Dissociable roles of the human somatosensory and superior temporal cortices for processing social face signals. *European Journal of Neuroscience, 20,* 3507–3515.

Roesch, E. B., Reveret, L., Grandjean, D., & Sander, D. (2006). *Generating synthetic, realistic, static and dynamic, FACS-based facial expressions.* Paper presented at the Proceedings of the Swiss Center in Affective Sciences.

Sander, D., Grafman, J., & Zalla, T. (2003). The human amygdala: An evolved system for relevance detection. *Reviews in the Neurosciences, 14,* 303–316.

Sander, D., Grandjean, D., Kaiser, S., Wehrle, T., & Scherer, K. R. (2007). Interaction effects of perceived gaze direction and dynamic facial expression: Evidence for appraisal theories of emotion. *European Journal of Cognitive Psychology, 19,* 470–480.

Sato, W., Kochiyama, T., Yoshikawa, S., Naito, E., & Matsumura, M. (2004). Enhanced neural activity in response to dynamic facial expressions of emotion: An fMRI study. *Cognitive Brain Research, 20,* 81–91.

Sato, W., Yoshikawa, S., Kochiyama, T., & Matsumura, M. (2004). The amygdala processes the emotional significance of facial expressions: An fMRI investigation using the interaction between expression and face direction. *Neuroimage, 22,* 1006–1013.

Scherer, K. R., & Ellgring, H. (2007). Are facial expressions of emotion produced by categorical affect programs or dynamically driven by appraisal? *Emotion, 7,* 113–130.

Smith, M. L., Cottrell, G. W., Gosselin, F., & Schyns, P. G. (2005). Transmitting and decoding facial expressions. *Psychological Science, 16,* 184–189.

Sprengelmeyer, R., Rausch, M., Eysel, U. T., & Przuntek, H. (1998). Neural structures associated with recognition of facial expressions of basic emotions. *Proceedings Biological Sciences/The Royal Society, 265,* 1927–1931.

Surguladze, S. A., Brammer, M. J., Young, A. W., Andrew, C., Travis, M. J., Williams, S. C., et al. (2003). A preferential increase in the extrastriate response to signals of danger. *Neuroimage, 19,* 1317–1328.

Todorovic, D. (2006). Geometrical basis of perception of gaze direction. *Vision Research, 46,* 3549–3562.

Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2001). Effects of attention and emotion on face processing in the human brain: An event-related fMRI study. *Neuron, 30,* 829–841.

Vuilleumier, P., Richardson, M. P., Armony, J. L., Driver, J., & Dolan, R. J. (2004). Distant influences of amygdala lesion on visual cortical activation during emotional face processing. *Nature Neuroscience, 7,* 1271–1278.

Whalen, P. J. (1998). Fear, vigilance, and ambiguity: Initial neuroimaging studies of the human amygdala. *Current Directions in Psychological Science, 7,* 177–188.

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