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Functional brain networks involved in gaze and emotional processing

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Abstract

Eye-gaze direction plays a fundamental role in the perception of facial features and particularly the processing of emotional facial expressions. Yet, the neural underpinnings of the integration of eye gaze and emotional facial cues are not well understood. The primary aim of this study was to delineate the functional networks that subserve the recognition of emotional expressions as a function of eye gaze. Participants were asked to identify happy, angry, or neutral faces, displayed with direct or averted gaze, whilst their neural responses were measured with fMRI. The results show that recognition of happy expressions, irrespective of eye-gaze direction, engages the critical nodes of the default mode network. Recognition of angry faces, on the other hand, is gaze-dependent, engaging the critical nodes of the salience network when presented with direct gaze, but fronto-parietal areas when presented with averted gaze. Functional connectivity analysis further showed gaze-dependent engagement of a large-scale network connected to bilateral amygdala during the recognition of angry expressions. This study provides important insights into the functional connectivity between the amygdala and other critical social-cognitive brain nodes, which are essential in processing of ambiguous, potentially threatening social signals. These findings have implications for psychiatric disorders, such as post-traumatic stress disorder, which are characterized by aberrant limbic connectivity.

Keywords: Amygdala, emotional expression, eye gaze, functional connectivity, multivariate analysis

Introduction

Eye-gaze perception plays a fundamental role in social and non-verbal communication, signaling one's intention to approach (direct gaze) or avoid (averted gaze) a person. Together with facial emotional cues, eye gaze carries important information about the underlying emotions and thus can enhance or disrupt perception of the expressed emotion. According to shared signal hypothesis (Adams & Kleck, 2005), when eye gaze matches the underlying emotion (e.g., angry expression with direct gaze), perception of that emotion would be enhanced. However, when eye gaze and emotion convey discordant information (e.g., angry expression with averted gaze), emotion perception would be diminished, possibly due to an increase in the ambiguity of social signaling. The ability to integrate diverse facial cues to determine others' intentions and affective or mental states is thus crucial to one's everyday social communication. Thus, understanding the functional networks of such highly complex processes will provide insights into the underlying mechanisms involved in social-cognitive and social functioning impairments among various psychiatric, neurological, and neurodegenerative illnesses (Burns, 2006; Kennedy & Adolphs, 2012; Yu & Wu, 2013).

A number of accounts have been proposed to explain the mechanisms involved in the processing of concomitant eye gaze and emotional expressions. According to the shared signal hypothesis, eye gaze and emotional cues share the congruent values of approach or avoidance tendencies and, therefore, should be processed more efficiently when they are both approach/avoidance congruent (Adams & Kleck, 2005). Alternatively, the proponents of the self-relevance appraisal hypothesis argue that facial cues are appraised according to their relevance to the observers' needs, goals, and well-being and thus should be processed more efficiently when the cues are

perceived as more self-relevant (Sander, Grandjean, Kaiser, Wehrle, & Scherer, 2007). Neuroimaging and lesion-based studies have provided support for both of these accounts and highlighted the importance of the amygdala in the integration of emotional cues with eye-gaze cues. Although some studies have reported the role of the amygdala in the recognition of angry emotion with direct eye gaze (Cristinzio, N'Diaye, Seeck, Vuilleumier, & Sander, 2010; N'Diaye, Sander, & Vuilleumier, 2009; Sander et al., 2007; Sato, Kochiyama, Uono, & Yoshikawa, 2010), others have found the opposite results, showing enhanced activity in the amygdala when presented angry emotion with averted eye gaze (Adams et al., 2012; Adams, Gordon, Baird, Ambady, & Kleck, 2003; Adams & Kleck, 2005). Besides these inconsistencies, only a few studies assessed such emotion-gaze interactions for happy expressions, with disparate results. Adams and Kleck, (2005 found enhanced recognition of happiness with direct gaze; however, Cristinzio et al., (2010 and Sander et al., (2007 did not find significant differences in the intensity rating of happy facial expressions as a function of eye-gaze orientation. Although parts of discrepancies reflect differences in the paradigm used in abovementioned studies, the underlying neural circuitry of emotion-gaze integration is still under investigated. Therefore, the primary aim of this study was to examine whole-brain activity during the recognition of happy and angry facial expressions as a function of eye gaze. Given that gazes are used as indicators of an expresser's attentional orientation (Sander et al., 2007), we treated the eye-gaze cues as means of conveying signals by a target face, and not what the observers felt, similar to Adams and Kleck, (2005.

Although amygdala has been considered a major hub for different social processes, e.g., social perception or social attribution (Bickart, Dickerson, & Barrett, 2014), it is still unclear to which brain regions amygdala is functionally connected

when processing socially-relevant and communicative signals. As the ability to understand and integrate socially-relevant cues is essential for social cognition, these processes undoubtedly rely on a large number of brain structures and their connections (Kennedy & Adolphs, 2012). In other words, given the complexity of the underlying cognitive integration of emotion and eye gaze, it is reasonable to suggest that these processes would be supported by a large-scale, distributed functional network. However, to our knowledge, no existing empirical research has examined functional connectivity of the amygdala during recognition of eye-gaze and emotional expressions cues. Thus, the second aim of this study was to delineate a task-related network that is functionally connected to bilateral amygdala and to assess the strength of connectivity within this network as a function of eye gaze. Delineating the amygdala network that is underlying critical social-cognitive processes may aid our understanding of the markers of social functioning.

Methods

Participants

Twenty-one healthy young adults (age 17-27 years, $M = 20.65$, $SD = 2.66$, 10 males) participated in this study. One participant was excluded from the whole-brain analysis due to extensive movement and two participants were removed from the connectivity analysis due to outlier nature of the brain signals. All participants were undergraduate students recruited from the University of Queensland in exchange for course credit or \$15 AUD per hour. Participants were screened for claustrophobia, neurological and psychiatric disorders, and magnetic resonance imaging (MRI) compatibility. All participants were right-handed, English speakers, had normal or corrected-to-normal vision, and had no history of neurological impairment or

psychiatric illnesses. They took part in two separate testing sessions: neuropsychological assessment and functional MRI (fMRI) scanning session. Participants were provided with a written consent as approved by the Human Research Ethics Committee at the University of Queensland and were debriefed upon the completion of the second session.

Materials

The stimuli consisted of color, front-view faces selected from the FACES database (Ebner, Riediger, & Lindenberger, 2010) and included happy, angry, and neutral expressions. The gazes of the posers were photoshopped toward either the right or the left side. All faces were categorized into five lists, using MATLAB (The MathWorks Inc., MA), according to the following selection criteria: gender of the posers, gaze direction, and emotional expression. The face presentation lists consisted of equal numbers of male and female posers (30 each), and emotional expressions (20 for each expression) and were presented in each fMRI run for a total of five runs. The order of the runs was counterbalanced among participants. Each face identity was presented once within a run, with only one emotional expression displayed within each run. Faces in each list were matched based on independent ratings of attractiveness ($M = 41.66$, $SD = 13.08$; Ebner et al., (2010)). In order to avoid habituation toward the faces, no more than two faces of each category (age of the face, facial expressions, and gaze direction) were repeated in a row. The faces were presented in 600 x 450 pixels, which were adjusted for the presentation in the scanner and presented against gray background, using E-prime software.

Experimental design

The scanner session lasted for 50 minutes and consisted of two components: structural MRI (sMRI) and fMRI during an emotion recognition task. Prior to the scanning, participants were verbally and visually instructed about the task and practiced until they were familiarized with the instructions. During the emotion recognition task in the scanner, participants were asked to identify, as fast and accurate as possible, whether the faces displayed happy, angry, or neutral expressions by pressing the relevant buttons on an MRI-compatible response box. Each face was presented, one at a time, for 3.5 seconds, followed by a fixation cross, which was randomly jittered using three time intervals: 0.5 seconds (20 trials), 1 seconds (20 trials), and 1.5 seconds (20 trials). The jittered inter-stimulus interval allowed for an independent estimation of the BOLD response on a trial-by-trial basis (Huettel, Song, & McCarthy, 2014). The task consisted of five runs of the emotion recognition task; each run lasted for 4.5 minutes. Participants performed two runs of the emotion recognition task, which was followed by an acquisition of sMRI. Then participants performed another three runs of the emotion recognition task.

Given the distinguished feature of happy expression, teeth showing, eye-tracking data were acquired during the behavioural session to ensure that (a) participants were examining all regions of the faces, including the eyes, and (b) there were not significant differences in inspecting mouth and eye regions of the faces for different emotional expressions. For further information on the eye-tracking data, please see Supplementary materials.

Image Acquisition, Preprocessing, and Analysis

Functional images were acquired at the Centre for Advanced Imaging using a 3-T Siemens scanner with a 32-channel head coil. The functional images were obtained using a whole-head T2*-weighted echo-planar image (EPI) sequence (93 slices,

repetition time (TR) = 3000ms, echo time (TE) = 45ms, flip angle = 90°, field of view (FOV) = 192mm, voxel size = 2mm³). High-resolution T1-weighted images were acquired with a MPRAGE sequence (126 slices with 1mm thickness, TR = 1900ms, TE = 2.3ms, TI = 900ms, FOV = 230ms, voxel size = 0.9mm³). The tasks were presented to participants on a computer screen through a mirror mounted on top of the head coil. Participants were provided with earplugs and cushions inside the head coil to dampen noise and minimize head movement.

For functional analysis, T2*-weighted images were pre-processed with Statistical Parametric Mapping Software (SPM8; <http://www.fil.ion.ucl.ac.uk/spm>) implemented in MATLAB 2010b (Mathworks Inc., MA). Following the realignment to a mean image for head-motion correction, images were segmented to gray and white matter. Then, images were spatially normalized into a standard stereotaxic space with a voxel size of 2mm³, using the Montreal Neurological Institute (MNI) template, and spatially smoothed with a 6-mm³ Gaussian Kernel.

The procedure of the fMRI analysis was twofold. First, we examined the whole-brain activity during emotion recognition of faces displayed with direct or averted gaze. For this purpose, we conducted a whole-brain analysis in which the BOLD response for the whole brain was measured across the experimental conditions. Second, we examined the connectivity of the functional network underlying emotion recognition of faces with direct and averted gaze. For this purpose, we selected bilateral amygdala as the seed region and correlated its BOLD intensity with that of the rest of the brain.

The fMRI data were statistically analyzed using a the multivariate analytical technique Partial Least Squares (PLS; McIntosh, Bookstein, Haxby, and Grady, (1996; McIntosh, Chau, and Protzner, (2004); for a detailed tutorial and review of

PLS, see Krishnan, Williams, McIntosh, and Abdi, (2011, running on MATLAB 2010b (The MathWorks Inc., MA). PLS analysis uses singular value decomposition (SVD) of a single matrix that contains all participants' data to find a set of orthogonal latent variables (LVs), which represent linear combinations of the original variables. Therefore, PLS enables differentiation of the degree of contribution of different brain regions associated with task demands, behavioral or anatomical covariates, or functional seed activity. The first LV usually accounts for the largest covariance in the data, with progressively smaller amounts for subsequent LVs. Each LV delineates a cohesive pattern of brain activity related to experimental conditions. Additionally, brain scores are calculated as the dot product of a subject's image volume of each LV. The brain score reflects how strongly each subject contributes to the pattern expressed in each LV. Each LV consists of a singular image of voxel saliences (*i.e.*, a spatiotemporal pattern of brain activity), a singular profile of task saliences (*i.e.*, a set of weights that indicate how brain activity in the singular image is related to the experimental conditions, functional seeds, or behavioral/anatomical covariates), and a singular value (*i.e.*, the amount of covariance accounted for by the LV). Given that the task was event-related, the analysis was conducted on the 15-sec period (5 TRs), starting at the onset of the faces, and activity at each time point in the analysis was normalized to activity in the first TR (labeled 0 in the Figure 3). The PLS analysis for the event-related data reveals a set of brain regions related to the task for each TR on each LV. For each TR, the pattern of brain activity identified for that TR is calculated for each participant. Mean brain scores across participants and across the entire brain are then plotted across the 5 TRs used in the analysis (Figure 3).

The statistical significance of each LV is assessed using permutation test, which determines that the probability of a singular value from 500 random reordering and

resampling is larger than initial obtained value (McIntosh et al., 1996). In addition to the permutation test, to determine the reliability of the salience for each brain voxel, a standard error of each voxel's salience on each LV is estimated by 100 bootstrap resampling steps (Efron & Tibshirani, 1985). Peak voxels with a bootstrap ratio (BSR; *i.e.*, salience/standard error) > 2.5 were considered to be reliable, as these approximate $p < 0.01$ (Sampson, Streissguth, Barr, & Bookstein, 1989). As the activation patterns identified by PLS and corresponding brain responses is done in one single step, therefore, there is no need for multiple comparison correction only.

Whole-Brain Analysis

We assessed whether emotion recognition is modulated by eye gaze and identified the specific functional loci for an a-priori selected anatomical region (amygdala) by examining whole-brain activations for two emotional expressions (angry and happy) and two eye-gaze directions (averted and direct). Neutral faces were utilized in the experimental design as a control condition, in order to remove the effect of visual perception (for a review see Sabatinelli et al., (2011)). A separate set of analysis included neutral conditions and revealed two main findings. First, the brain networks involved for happy and angry expressions did not change as a matter of including neutral conditions in the analysis. Second, the salience network, including anterior cingulate gyrus and bilateral insula, was involved during recognition of neutral expressions irrespective of the eye gaze. However, given that previous works also found that the ambiguity of neutral faces may lead to uncertainty and heightened vigilance, which, in turn, may increase amygdala activity (Blasi et al., 2009), all of the analyses in the results section were reported only for recognition of happy and angry facial expressions.

Functional Connectivity

We also examined task-related functional connectivity during angry emotional expressions for direct and averted gaze by correlating activity in bilateral amygdala with activity in the rest of the brain during angry emotion recognition. Although amygdala activity has been reported in processing of happy facial expressions (Canli, Sivers, Whitfield, Gotlib, & Gabrieli, 2002), we did not find any amygdala activity in the whole-brain findings during happy facial recognition; thus, we conducted the functional connectivity analyses on the angry expression conditions only.

The selection of bilateral amygdala was based on two criteria: first, theoretical – previous studies have highlighted the critical role of bilateral amygdala in gaze and emotional processing (Calder & Young, 2005; Carlin & Calder, 2013; Itier & Batty, 2009; Shepherd, 2010); and second, data-driven – in the whole-brain analysis we identified the functional loci for the a-priori amygdala regions, left (MNI: -18 -4 -12) and right (MNI: 20 -8 -12) during recognition of angry expressions. To delineate the functional network involved during gaze and emotional processing, we extracted the BOLD values from the peak voxels of the seed regions for the angry conditions and correlated them with activity in the rest of the brain across all participants. These correlations were then combined into a matrix and decomposed with singular value decomposition. This resulted in a set of LVs characterizing the set of regions where activity was correlated with seed activity during direct or averted gaze conditions. The significance and reliability of the analysis were determined by permutation test and bootstrap sampling, as described above.

Results

Behavioral Results

A 2 (eye-gaze directions: direct and averted) by 2 (emotions: happy and angry) repeated measures ANOVA on accuracy revealed a significant main effect of emotion, $F = (1, 18) = 13.01$, $p < .01$, $\eta_p^2 = .42$, with higher accuracy for happy than angry faces. A similar analysis was conducted for the response times (RT). Due to the long RT (+3 SD more than the group mean), one participant was excluded from the analysis performed on RTs. A significant main effect of emotion, $F = (1,17) = 34.47$, $p < .001$, $\eta_p^2 = .67$, suggests that happy faces were recognized faster than angry faces. No significant main effect of gaze or interactions between emotion and eye-gaze directions were found for RTs or accuracy (all F s < 1).

[Insert Figure 1 about here]

Whole-brain Results

Recognition of angry expressions

The results from whole-brain analyses delineated two significant LVs. LV1 accounted for 48% of covariance in the data and revealed a set of brain regions, which were engaged during the processing of angry averted conditions relative to the other conditions. In line with our first prediction, this set of regions included bilateral amygdala as well as bilateral inferior frontal gyrus (IFG), right middle frontal gyrus, bilateral superior frontal gyrus, medial frontal gyrus, left cingulate gyrus, bilateral inferior parietal lobe (IPL), bilateral insula, left superior temporal gyrus (STG), putamen, bilateral thalamus, and bilateral cuneus (Fig. 2, Panel A & Table 2). LV2 accounted for 33% of covariance in the data, revealing a set of regions with increased activity during recognition of angry direct faces relative to the other conditions (Fig.

2, Panel B & Table 3). These areas included right superior frontal gyrus, right cingulate gyrus, right middle temporal gyrus, right superior parietal lobe, bilateral occipital gyrus, bilateral insula, bilateral putamen, and left amygdala.

Recognition of happy expressions

In contrast, recognition of happy facial expressions with both direct and averted gaze directions activated bilateral anterior cingulate gyrus, left medial frontal gyrus, bilateral superior frontal gyrus, bilateral middle temporal gyrus, left IPL, bilateral superior parietal lobe, left precuneus, and left posterior cingulate cortex (PCC; Fig. 2, Panel C & Table 3).

[Insert Figure 2 and Tables 2&3 here]

Given the role of amygdala in processing emotional expressions and eye-gaze cues, we extracted and compared the time courses of the amygdala during recognition of angry with averted relative to direct gaze conditions. During the recognition of angry expression with averted gaze condition, activity in left amygdala peaked around 6 seconds, whereas activity in right amygdala showed a more sustained activation during recognition of angry averted condition relative to the angry direct condition (Fig. 3). A series of independent *t*-tests showed significant differences between signal intensity of right and left amygdala at time points 3, 6, and 9-sec after stimulus onset during recognition of angry expressions with averted gaze relative to the angry expressions with direct gaze, all *ps* < .05.

[Insert Figure 3 here]

Functional Connectivity of the Amygdala

The results from the seed PLS analysis revealed one significant LV, which explained 67% of covariance in the data and delineated a functional network

connected to bilateral amygdala. This functional network was engaged significantly more strongly during recognition of angry faces with averted gaze than it was during recognition of angry emotion with direct gaze (Fig. 4 & Table 4). This network included bilateral middle frontal gyrus, bilateral superior frontal gyrus, right anterior cingulate gyrus, right inferior frontal gyrus, bilateral STG, bilateral PCC, left IPL, precuneus, and bilateral thalamus.

[Insert Figure 4 and Table 4 here]

Discussion

The aims of the study were to examine whole-brain activity and functional connectivity during emotion recognition of faces displayed with direct or averted eye gaze. Three primary findings emerged: i) although participants did not show any modulation of eye gaze for happy expressions, recognition of angry expressions was modulated by the direction of eye gaze; ii) in line with some previous works (Adams et al., 2012; Adams et al., 2003; Adams & Kleck, 2005), bilateral amygdala was involved significantly more strongly during the recognition of angry faces with *averted* gaze than angry faces with direct gaze; and iii) functional connectivity results revealed a social-cognitive network, which was connected to bilateral amygdala significantly more strongly during the recognition of angry faces with averted gaze than angry faces with direct gaze. These findings show that the discriminability of facial expressions plays a critical role in the processing of concomitant eye gaze and emotion expressions, and provide evidence for a functional amygdala network, which integrates information of eye gaze and emotion of particularly ambiguous stimuli.

Recognition of angry expressions with direct gaze

During the recognition of angry expressions with direct gaze, the whole-brain analysis showed activity in the insula and dorsal anterior cingulate cortex (ACC), critical nodes of the salience network. The salience network is known to be important in orienting and allocating cognitive control resources toward subsequent stimulus processing (Barrett & Satpute, 2013) and orienting attention towards them in order to adaptively guide behavior (Menon, 2015). The engagement of the salience network during the recognition of angry expressions suggests that these regions are essential in orienting cognitive resources toward threatening stimuli. Moreover, the engagement of anterior insula during the processing of angry expressions with direct gaze is in line with previous studies that show the involvement of this region in a wide range of cognitive (Desimone & Duncan, 1995; Hopfinger, Buonocore, & Mangun, 2000; Menon & Uddin, 2010) and emotional (Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012; Ochsner & Gross, 2005) tasks. Anterior insula constitutes a hub of the ventral attentional network, which communicates salient information to other cortical and subcortical networks in order to evaluate and switch between cognitive networks (Menon & Uddin, 2010; Sridharan, Levitin, & Menon, 2008). It is thus not surprising that the anterior insula, and in general, the salience network, is engaged more strongly during the processing of angry direct faces in order to orient attentional resources toward a threatening stimulus.

Recognition of angry expressions with averted gaze

In contrast to recognition of angry emotion with direct gaze, recognition of angry facial expression with averted gaze engaged frontal and parietal regions, as well as bilateral amygdala. This finding is in line with previous findings showing amygdala activity during angry expressions with averted gaze (Adams et al., 2003), but is in contradiction with other studies that showed increased activity of amygdala

in response to angry faces with direct gaze (N'Diaye et al., 2009; Sato, Yoshikawa, Kochiyama, & Matsumura, 2004). It must be acknowledged, however, that the differences in stimulus presentation duration and stimulus set across studies might be contributing to such discrepancies. In order to reconcile these differences across discrepant studies, Adams et al., (2012) conducted several experiments in which different stimulus sets (Ekman faces and NimStim faces) and different presentation durations were employed (1-sec vs. 300-msec), with participants passively viewing the stimuli. Their findings demonstrate that amygdala shows an early, reflexive response toward a clear threat (angry direct gaze), but is more tuned toward ambiguous threat (angry averted gaze) at a later, reflective response. In addition, our study lends support to the notion that task instructions in emotion recognition research are critically important. Using an explicit emotion recognition task as in the present study, we found amygdala to be engaged during recognition of angry averted gaze. This finding supports the idea that amygdala subserves the processing of highly ambiguous signals as conveyed by the combination of angry facial expressions and averted gaze using naturalistic stimuli, such as those from the FACES database.

Functional brain networks during recognition of angry expressions

In addition to the gaze-dependent differentiation of regional activations during the recognition of angry facial expressions, functional connectivity results revealed a large-scale network whose connectivity was significantly stronger during the recognition of angry averted than angry direct faces. In addition to bilateral amygdala, this network included IPL, STS, and medial PFC (mPFC), the critical nodes of the social brain network. Activity in STS and mPFC has been reported in a variety of tasks, such as social cognition (Allison, Puce, & McCarthy, 2000), emotion processing and eye gaze (N'Diaye et al., 2009; Pourtois et al., 2004), biological

motion perception (Pelphrey & Morris, 2006; Vander Wyk, Hudac, Carter, Sobel, & Pelphrey, 2009), as well as perspective taking (Gallagher & Frith, 2003; Mitchell, Banaji, & MacRae, 2005; Molenberghs, Johnson, Henry, & Mattingley, 2016; Saxe & Powell, 2006). Thus, we interpret the strong connectivity of STS and mPFC with bilateral amygdala during the recognition of angry averted gaze in line with the idea that averted gaze is ambiguous and may require significantly more inference of the mental state of others than direct gaze does. Therefore, recognition of angry emotions with averted gaze relies on a distributed social brain network, which is functionally connected to the amygdala. The identified functional network for angry averted gaze resembles the subnetwork of the social brain that has been shown to be involved in detecting socially salient stimuli (Kennedy & Adolphs, 2012). Our results extend these findings and suggest that the functional network connected to the amygdala is strongly involved during recognition of salient, ambiguous, and socially-communicative cues. The connection between brain regions from core (e.g., STS and fusiform gyrus) as well as extended systems (e.g., mPFC, IPL, insula, precuneus, and striatum) and the amygdala indicates the integration of these two systems at higher social-cognitive processes (Haxby & Gobbini, 2011). Therefore, our results extend findings from previous literature by showing that recognizing threat in an ambiguous situation from facial cues relies strongly on the functional network of the amygdala. Future studies are required to provide further insight into the changes occur in the functional network of amygdala in psychiatric and neurological illnesses and to determine the extent to which changes in this network are associated with deficits in social functioning among patients.

Recognition of happy expressions

Recognition of happy expressions, however, was not modulated by eye-gaze directions at either behavioral or neural levels, in line with previous behavioral studies, which show that recognition of happy facial expressions are insensitive to gaze modulation (N'Diaye et al., 2009; Sander et al., 2007). This finding could be explained in line with the speed-of-processing hypothesis, which states that the distinguished features of happy facial expressions – e.g., teeth showing – make the recognition of happy expression easier and could prevent the interference from the eye regions (Graham & Labar, 2012). Regardless of gaze, we show that recognition of happy expressions engaged the critical nodes of the default mode network (DMN; e.g., vmPFC, PCC, precuneus, and STS; Raichle et al., 2001). DMN is involved in perspective-taking of desire, beliefs, and intentions of others, i.e., processes that are self-referential in nature (Buckner, Andrews-Hanna, & Schacter, 2008). This network has an extensive connectivity with regions involved in emotion processing (Grimm et al., 2009; Sheline et al., 2009) and social function (Kennedy & Adolphs, 2012; Mars et al., 2012), and is mainly engaged when task demands decrease (Buckner et al., 2008; Mckiernan, Kaufman, Kucera-Thompson, & Binder, 2003). Our results therefore suggest that recognition of happy expressions may be easier and imposes lower demands on cognitive resources relative to recognition of angry expressions and, as a result, recognition of happy expressions may rely more heavily on self-referencing processes subserved by the DMN. Recognition of angry expressions, however, may require more cognitive effort than happy expressions, engaging areas beyond the DMN, such as IFG.

There is a methodological consideration that has to be highlighted here. Participants in our study were asked to identify the emotional expressions of the faces rather than gender or emotion intensity ratings. Previous studies that did not find

effects of gaze modulation for happy expressions used intensity ratings (Cristinzio et al., 2010; Sander et al., 2007). Thus, the task instruction might have an impact on the interplay between eye gaze and emotional expressions. We speculate that asking participants to focus on variant or invariant features of the face might have differential impact on the recruitment and interaction between core and extended systems (Haxby & Gobbini, 2007). Therefore, future research is required to investigate the impact of different task instruction on the interplay between eye gaze and emotional expressions. Additionally, although we did not find any amygdala activity for happy expressions, previous studies reported the engagement of this region for processing happy facial cues (e.g., Canli, Sivers, Whitfield, Gotlib, & Gabrieli (2002)). Future studies are needed to investigate the role of amygdala network during recognizing happy expressions and integrating other facial communicative cues from happy expressions.

In conclusion, the current study examined the underlying neural mechanisms involved in the recognition of emotional expressions displayed with direct or averted gaze. The findings suggest that the brain activity involved in the recognition of angry expressions is modulated by eye-gaze direction, whereas recognition of happy expressions is not influenced by eye gaze. The results imply that the valence and discriminability of stimuli are critical factors in understanding eye gaze and facial emotion interactions. Moreover, we identified a functional network, which comprises bilateral amygdala and the main nodes of the social-cognitive network, which seem critical to the processing of ambiguous and potentially threatening social signals (like angry averted faces). These findings provide an insight into the underlying functional networks involved in processing socially communicative signals. The results from this

study have a potential to inform clinical investigations of psychiatric and neurological illnesses that are characterized by social cognitive impairments.

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Table 1

Descriptive statistics for the background cognitive measures

<i>Measure</i>	<i>M</i>	<i>SD</i>
NART FSIQ (Nelson, 1982)	113.75	3.84
Age	20.65	2.66
RMET (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001)	27.47	1.94
Ekman emotion recognition (Young, Perrett, Calder, Sprengelmeyer, & Ekman, 2002)		
<i>Sadness</i>	7.78	1.81
<i>Disgust</i>	7.68	1.56
<i>Happiness</i>	9.60	0.58
<i>Surprise</i>	9.15	1.06
<i>Fear</i>	7.21	2.55
<i>Anger</i>	7.36	1.64
PRSF (Henry, von Hippel, & Baynes, 2009)		
<i>Social Inappropriateness</i>	19.73	4.90
<i>Social Appropriateness</i>	58.10	6.90
<i>Prejudice</i>	6.84	1.06
Empathy Quotient (Baron-Cohen & Wheelwright, 2004)	42.16	10.35
Big Five Inventory (John & Srivastava, 1999)		
<i>Extraversion</i>	27.89	6.05
<i>Agreeableness</i>	31.31	3.41
<i>Conscientiousness</i>	30.78	5.66
<i>Neuroticism</i>	21.10	6.17
<i>Openness</i>	33.36	6.29

Note. NART FSIQ = National Adult Reading Test Full-Scale Intelligence Quotient, RMET = Reading the Mind in the Eye Test, PRSF = Peer-Report Social Functioning Scale.

Table 2

Regions from LV1 of whole-brain analysis showing increased activity for recognition of angry facial expression with averted gaze vs. all other conditions

Regions	Hem	BA	MNI coordinates	BSR
			XYZ	
Medial Frontal Gyrus	L	6	[0 2 56]	6.22
Superior Frontal Gyrus	L	9	[-36 50 24]	5.03
	R	9	[38 50 26]	3.74
Inferior Frontal Gyrus	R	46	[52 36 10]	7.40
	L	9	[-60 10 24]	6.67
Anterior Cingulate Gyrus	L	32	[-2 14 40]	4.92
Superior Temporal Gyrus	L	22	[-56 6 2]	6.67
Inferior Parietal Lobe	L	40	[-56 -16 26]	5.52
	R	40	[64 -32 26]	4.02
Precentral Gyrus	L	43	[-54 -2 10]	6.13
	R	44	[56 10 0]	6.04
Postcentral Gyrus	R	3	[58 -12 28]	6.25
	L	3	[-44 -14 58]	6.82
Posterior Cingulate Gyrus	L	23	[-2 28 28]	4.59
Posterior Cingulate Gyrus	R	30	[12 -60 6]	5.95
	L	30	[-12 -68 8]	4.58
Middle Occipital Gyrus	R	18	[32 -86 -2]	8.39
	L	19	[-34 -88 4]	6.03
Cuneus	L	23	[-6 -72 12]	4.97
Insula	L	13	[-46 -2 4]	6.35
	R	13	[48 6 0]	6.1
Putamen	L		[-28 -2 10]	5.4
Thalamus	L		[-8 -20 10]	4.93
	R		[10 -14 10]	4.22
Amygdala	L		[-18 -4 -12]	5.34
	R		[20 -8 -12]	3.19
Cerebellum	L		[-25 -70 -15]	4.57
	R		[36 -55 -15]	5.88

Note. BSR = Bootstrap Ratio, $BSR \geq 2.5$, $p < .005$; Hem = Hemisphere; R = right; L = left; BA = Brodmann Area; x coordinate = right/left; y coordinate = anterior/posterior; z coordinate = superior/inferior.

Table 3

Regions from LV2 of whole-brain analysis showing increased activity for recognition of angry facial expressions with *direct* gaze and happy facial expressions with both direct and averted gaze relative to the other conditions

Regions	Hem	BA	MNI coordinates	BSR
			XYZ	
Angry facial expression (direct gaze) > happy facial expressions				
Superior Frontal Gyrus	R	6	[4 20 46]	4.99
Anterior Cingulate Gyrus	R	32	[0 22 39]	3.94
Middle Temporal Gyrus	R	37	[46 -62 0]	4.69
Superior Parietal Lobe	R	7	[26 -58 47]	6.32
Occipital Gyrus	R	19	[36 -80 0]	3.7
	L	19	[-46 -76 -4]	4.8
Insula	R	13	[44 20 2]	4.6
	L	13	[-42 14 2]	4.8
Amygdala	L		[-24 -12 -15]	3.90
Putamen	R		[24 6 6]	3.64
	L		[-26 2 6]	3.73
Cerebellum	R		[40 -68 -8]	4.65
	L		[-46 -76 -6]	5.56
Happy facial expression (direct & averted gaze) > angry facial expressions				
Middle Frontal Gyrus	L	6	[-26 2 48]	5.31
Superior Frontal Gyrus	R	8	[26 30 46]	3.68
	L	8	[-24 34 46]	3.7
Medial Frontal Gyrus	L	32	[-6 16 48]	5.82
Anterior Cingulate Gyrus	R	24	[2 30 -14]	4.51
	L	32	[-10 42 -6]	5.78
Middle Temporal Gyrus	R	39	[46 -70 30]	3.65
	L	39	[-48 -70 30]	4.23
Middle Temporal Gyrus	L	21/ 22	[-58 -32 2]	8.51
Superior Parietal Lobe	R	7	[28 -56 62]	5.18

	L	7	[-26 -64 56]	5.56
Inferior Parietal Lobe	L	7	[-32 -52 48]	4.73
	L	40	[-50 -36 48]	5.18
Posterior Cingulate Gyrus	L	31	[-8 -34 46]	3.77
Precuneus	L	31	[-12 -62 24]	4.58

Note. BSR = Bootstrap Ratio, $BSR \geq 2.5$, $p < .005$; Hem = Hemisphere; R = right; L = left; BA = Brodmann Area; x coordinate = right/left; y coordinate = anterior/posterior; z coordinate = superior/inferior.

Table 4

Regions from functional connectivity with bilateral amygdala for recognition of angry facial expressions

Regions	Hem	BA	MNI coordinates	BSR
			XYZ	
Middle Frontal Gyrus	R	46	[50 42 10]	7.68
	L	10/46	[-42 48 12]	5.17
Inferior Frontal Gyrus	R	44	[62 12 18]	5.92
Superior Frontal Gyrus	L	8	[-2 42 44]	5.71
	R	6	[5 12 56]	8.55
Middle Frontal Gyrus	L	9	[-43 26 27]	8.26
	L	8	[-26 26 46]	5.13
Anterior Cingulate Gyrus	R	24	[22 16 48]	9.22
Precentral Gyrus	R	6	[62 2 10]	7.33
	L	4	[-56 -2 18]	10.91
Superior Temporal Gyrus	R	22	[38 -52 16]	6.44
	L	38	[-43 10 -31]	8.55
Inferior Parietal Lobe	L	40	[-40 -50 54]	9.57
Postcentral Gyrus	R	40/43	[60 -18 18]	4.39
Posterior Cingulate Gyrus	L	23	[-2 28 28]	4.59
	R	31	[12 -62 18]	5.93
Fusiform Gyrus	R	37	[41 -59 -15]	5.47
Cuneus	R	18	[18 -68 18]	6.72
Precuneus	L	31	[-14 -66 18]	5.31
Caudate	L		[14 4 18]	9.33
Putamen	R		[-28 -2 10]	5.87
Thalamus	L		[-14 -28 12]	7.03
	R		[10 -14 10]	4.16
Cerebellum	L		[-16 -68 -15]	7.96
	R		[10 -63 -15]	6.26
Amygdala	R		[20 -8 -14]	19.33
	L		[-18 -4 -12]	12.33

Note. BSR = Bootstrap Ratio, $BSR \geq 2.5$, $p < .005$; Hem = Hemisphere; R = right; L = left; BA = Brodmann Area; x coordinate = right/ left; y coordinate = anterior/posterior; z coordinate = superior/inferior.

Figure Legends

Fig. 1. Behavioral Results. Behavioral results from the emotion recognition task. Participants were faster and more accurate for recognizing happy expressions relative to angry expressions. The bars represent 1 standard error of the mean (SEM).

Fig. 2. Whole-Brain Results. Patterns of whole-brain activity during the recognition of angry expressions with averted gaze (A), angry expression with direct gaze (B), and happy expression with direct and averted gaze (C), relative to the other conditions. Error bars denote 95% confidence intervals for the correlations calculated from the bootstrap procedure. All reported regions have $BSR \geq 2.5$ and cluster size ≥ 100 voxels. L = left hemisphere, R = right hemisphere.

Fig. 3. BOLD Signal Intensity in Bilateral Amygdala. Peak voxel intensity of left (-18 -4 -12) and right (20 -8 -12) amygdala during the four experimental conditions within 12-sec after stimulus onset. A series of independent *t*-tests showed significant differences between signal intensity of right and left amygdala at time points 3, 6, and 9-sec after stimulus onset during recognition of angry expressions with averted gaze relative to the angry expressions with direct gaze, all $ps < .05$.

Fig. 4. Functional Connectivity Results. (A) The functional network connected to bilateral amygdala during the angry conditions. (B) Correlations between activity in bilateral amygdala and the functional network during the angry conditions. Error bars denote 95% confidence intervals (CIs) for the correlations calculated from the bootstrap procedure. Brain/correlation scores were considered unreliable when CIs crossing zero and considered significantly different if CIs did not overlap. All reported regions have $BSR \geq 2.5$ and cluster size ≥ 100 voxels.

