Facial expression and gaze-direction in human superior temporal sulcus

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Abstract

The perception of facial expression and gaze-direction are important aspects of non-verbal communication. Expressions communicate the internal emotional state of others while gaze-direction offers clues to their attentional focus and future intentions. Cortical regions in the superior temporal sulcus (STS) play a central role in the perception of expression and gaze, but the extent to which the neural representations of these facial gestures are overlapping is unknown. In the current study 12 subjects observed neutral faces with direct-gaze, neutral faces with averted-gaze, or emotionally expressive faces with direct-gaze while we scanned their brains with functional magnetic resonance imaging (fMRI), allowing a comparison of the hemodynamic responses evoked by perception of expression and averted-gaze. The inferior occipital gyri, fusiform gyri, STS and inferior frontal gyrus were more strongly activated when subjects saw facial expressions than when they saw neutral faces. The right STS was more strongly activated by the perception of averted-gaze than direct-gaze faces. A comparison of the responses within right STS revealed that expression and averted-gaze activated distinct, though overlapping, regions of cortex. We propose that gaze-direction and expression are represented by dissociable overlapping neural systems.
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Humans are highly sensitive to non-verbal cues that provide important information about the emotional state, focus of attention, and future behavior of others (Simpson & Crandall, 1972). The accurate perception and analysis of these cues is an important component of 'social cognition' and facilitates appropriate behavior in complex social groups. Two particularly salient and powerful cues are facial expressions and gaze-direction. An individual's facial expression is a reliable and accessible indication of their internal emotional state (Ekman & Rosenberg, 2005). The importance of expressions as social signals is highlighted by evidence that their frequency and intensity increase in social situations (Fridlund, 1994; Jancke & Kaufmann, 1994). The gaze-direction of others communicates their current focus of attention and provides clues to their future intentions. The importance of this information is underscored by evidence that humans as young as 10 weeks old (Hood, Willen, & Driver, 1998), non-human great apes (Tomasello, Call, & Hare, 1998),

and monkeys (Emery, Lorincz, Perrett, Oram, & Baker, 1997) automatically orient their attention to the target of another's gaze (Friesen, Chris Kingstone, & Alan, 1998).

The brain regions responsible for the perception of facial identity and facial gesture have been shown to be largely dissociable both in the macaque (Hasselmo, Rolls, & Bayliss, 1989) and human (Andrews, & Ewbank, 2004; Engell, Gobbini, & Haxby, 2006; Hoffman & Haxby, 2000) cortex. Haxby, Hoffman, and Gobbini (2000) have, therefore, proposed a distributed human neural system for face perception that posits a primary role of the superior temporal sulcus (STS) in perception of dynamic facial features and a primary role of the ventral temporal cortex, including the fusiform gyrus, in the perception of facial features that are invariant over dynamic changes (i.e. identity).

Single-cell recording in monkeys (Hasselmo, Rolls, & Baylis, 1989) and humans (Ojemann, Ojemann, & Lettich, 1992), as well as human neuropsychological (Rapcsak, Kaszniak, & Rubens, 1989) and neuroimaging (Gur, Skolnick, & Gur, 1994; Narumoto, Okada, Sadato, Fukui, & Yonekura, 2001) studies, have all implicated the STS in expression processing. Similarly, the STS has been implicated in the perception of gaze-direction by single-cell recording in monkeys (Perrett et al., 1985), human

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neuroimaging (Hoffman & Haxby, 2000; Puce, Allison, Bentin, Gore, & McCarthy, 1998; Wicker, Michel, Henaff, & Decety, 1998), and human electrophysiological responses as measured with scalp (N170; Puce, Smith, & Allison, 2000) and intracranial (N200; Allison, Puce, Spencer, & McCarthy, 1999; McCarthy, Puce, Belger, & Allison, 1999) electrodes.

Despite this similarity, it is unknown if a single system supports the perception of both types of stimuli. Many recent studies have investigated the behavioral effect of gaze-direction on expression recognition (e.g. Adams & Kleck, 2003, 2005; Ganel, Goshen-Gottstein, & Goodale, 2005) and of facial expression on the reflexive orienting effects of gaze-direction (e.g. Holmes, Richards, & Green, 2006; Hori et al., 2005; Mathews, Fox, Yeind, & Calder, 2003; Putman, Hermans, & van Honk, 2006). These studies suggest a behavioral interdependence that is further supported by evidence that the amplitude of event-related potentials recorded from the scalp of 4-month olds is larger during perception of angry faces with direct-gaze than angry faces with averted-gaze (Striano, Kopp, Grossmann, & Reid, 2006; but see Pourtois et al., 2004). However, to date, there have been no direct comparisons of the neural response evoked within the STS by both expression and gaze-direction perception.

The objective of our study was to explore whether perception of facial expression and averted-gaze resulted in dissociable patterns of activity within the STS region of the lateral temporal cortex. Subjects viewed blocks of either neutral faces with direct-gaze ("control" condition), emotional faces with direct-gaze ("expression" condition), or neutral faces with averted-gaze ("averted-gaze" condition) while we scanned their brains with functional magnetic resonance imaging (fMRI). We examined the signal changes evoked by the perception of emotional faces and averted-gaze relative to the control condition to determine whether they shared a single neural substrate.

Both facial expression and gaze-direction represent facially communicated social information. However, we hypothesized that the observation of these two gestures would evoke dissociable neural representations due to the distinctiveness of each gesture's informational content (i.e. emotional state and target of attention, respectively). Further, we predicted that we would find this dissociation in the STS region given its putative role in processing facial gesture.

1. Materials and methods

1.1. Subjects

Thirteen participants (5 females and 7 males, age 22–33) were recruited from the community in and around Princeton University (Princeton, NJ). One subject was excluded from analysis due to excessive head motion. The participants were all right-handed and had normal or corrected vision. All participants gave informed consent prior to the experiment and were fully debriefed at its completion in accordance with the policies of Princeton University's Institutional Review Panel.

1.2. Stimuli

Pictures were taken from the Pictures of Facial Affect (Ekman & Friesen, 1976) and modified to display different gaze directions. The full stimulus set included 11 individuals posing in nine conditions. The nine conditions included

four emotional expressions (anger, disgust, fear, surprise) displaying a direct-gaze, four averted-gaze poses (full left, partial left, full right, partial right) displaying a neutral expression, and a neutral expression displaying a direct-gaze (Fig. 1a). The four basic expressions were selected in order to best mirror the confusability of the gaze stimuli. That is, just as full and partial gaze toward a given direction is presumably harder to distinguish than gaze to an opposite direction, the expressions of disgust and anger (and surprise and fear) are more likely to be confused for each other than for other expressions.

To create the averted-gaze images we used Adobe PhotoShop CS (Adobe, CA) on an Apple iMac G4 (Apple Computer, CA) to modify the original images from the Pictures of Facial Affect.

Visual stimuli were projected onto a screen at the rear of the bore of the magnet. Subjects viewed these images via an angled mirror attached to the RF coil and placed above their eyes.

1.3. Task

Each of the eight runs contained nine blocks of 14 face images. There was one block for each of the nine conditions in every run. Seven face images were presented twice in random order in each block. The faces selected for each block (7 of a possible 11) and the order of the nine blocks were randomized across runs.

All runs began with a 32-s presentation of a fixation cross. Faces were presented for 1 s. At the conclusion of each 14-s block, a black fixation cross would appear on a white screen for 1 s immediately followed for 1 s by another face (the "test face") with the same expression and gaze-direction as the images in preceding block (Fig. 1b). The participant's task was to report whether the identity of the test face was the same as any of the faces in that block. The experimenter monitored responses during the acquisition periods to ensure participants were engaged in the task but were not recorded, as they were orthogonal to the perception of expression or gaze. Each of these blocks was separated by a 16-s rest period in order to allow hemodynamic activity to return to baseline levels.

1.4. Image acquisition

The blood oxygenation level-dependent (BOLD) signal was used as a measure of neural activation (Kwong et al., 1992; Ogawa, Lee, Kay, & Tank, 1990). Echo planar images (EPI) were acquired with a Siemens 3.0 Tesla Allegra head-dedicated scanner (Siemens, Erlangen, Germany) with a standard "bird-cage" head coil (TR, 2000 ms, TE, 30 ms, flip angle, 90°, matrix size, 64 × 64). Near whole brain coverage was achieved with 33 interleaved 3-mm axial slices. At the beginning of each scan session a high resolution anatomical image (T1-MPRAGE, TR, 2500 ms, TE, 4.3 ms, flip angle, 8°, matrix size 256 × 256) was acquired for use in registering activity to each subject's anatomy and for spatially normalizing data across subjects.

1.5. Preprocessing

Data was analyzed with Analysis of Functional NeuroImages (AFNI; Cox, 1996) using standard preprocessing procedures. These procedures included 6 parameter 3D motion-correction, undistortion (Cusack, Brett, & Osswald, 2003), spatial smoothing with a 6-mm full-width-at-half-minimum Gaussian kernel and signal normalization to percent signal change from the mean.

1.6. Image analysis

Each of the eight time-series was convolved with a hemodynamic response function to create a regressor for each of the nine facial configuration conditions. Regressors of non-interest were included in the multiple regression model to factor out variance associated with mean, linear, and quadratic trends in each run as well as subject head motion. The regression model yielded coefficients that represented the signal change from the mean for each condition within each voxel.

We tested three linear contrasts. In the expression minus control contrast, all four of the expression conditions (anger, disgust, fear, and surprise) were contrasted with the control condition to find regions that were more strongly
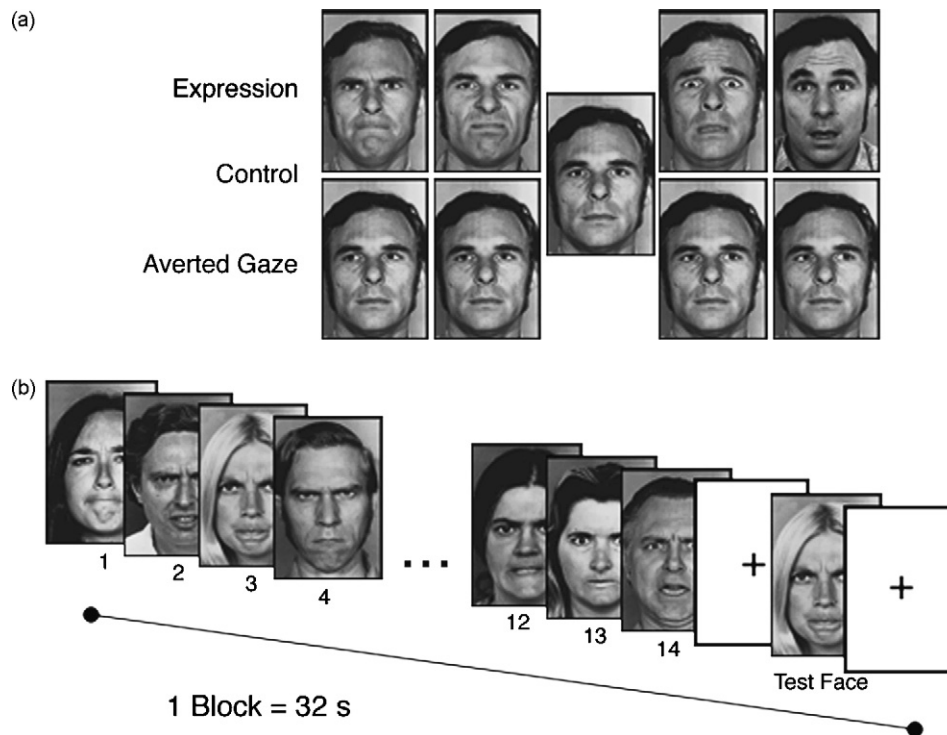
Fig. 1. (a) Example expression stimuli. From left to right: anger, disgust, neutral, fear, surprise (top row). Example control stimulus (center row). Example gaze stimuli (bottom row). From left to right: full right, partial right, direct, partial left, full left. (b) Example stimulus presentation block. Each block comprised a series of 14 pictures presented for 1 s each. The 14 faces were immediately followed by a fixation cross and a "test face" (see Section 1) presented sequentially for 1 s each. Each block concluded with a 16 s presentation of a fixation cross.

activated by expression than by a neutral face. In the averted-gaze minus control contrast, all four of the averted-gaze conditions (full left, partial left, full right, partial right) were contrasted with the control condition to find regions that were more strongly activated by averted-gaze than by direct-gaze. In the expression minus averted-gaze contrast, all four examples of emotional faces were contrasted with all four examples of averted-gaze to identify regions that were more strongly activated by expression or averted-gaze as compared to the other.

The nine-parameter landmark method of Talairach and Tournoux (1988) was used in order to spatially normalize the activation maps across subjects. A random effects analysis of variance (ANOVA) was performed on the coefficients supplied by the multiple regression analysis to test the significance of contrasts across all subjects. We used the AlphaSim program, included in AFNI, to correct for multiple comparisons. A minimum cluster size of $1890\,mm^3$ to achieve corrected significance of $p < 0.05$ was determined by a Monte Carlo simulation with a voxel-wise threshold of $p < 0.005$.

1.7. Signal time-course analysis

Time courses of the hemodynamic responses were created to further illustrate the response profiles of voxels within the lateral and ventral cortices. Preprocessing for time-course analysis consisted of motion-correction, removal of linear and quadratic trends from the data, and conversion to percent signal change from baseline (as defined by average signal level during rest).

The right posterior lateral temporal cortex, which includes the posterior STS, was anatomically defined in each subject. We created three time courses of the average signal for the voxels that were only expression-selective, only averted-gaze selective, and selective to both expression and averted-gaze ($p < 0.05$, uncorrected). One subject did not have any voxels representing an overlap between expression greater than control and averted-gaze greater than control. The average of the activity from 6 to 14 s after stimulus onset was used for t-tests of statistical significance.

In order to examine the effect of expression and averted-gaze within face responsive ventral temporal cortex the event-related signal for expression, con-

trol, and averted-gaze blocks were extracted from face responsive voxels defined by an omnibus test of the combined effect of all regressors of interest ($F > 100$) from within anatomically defined masks of this region.

2. Results

2.1. General linear model results

All reported activations are significant at a p level of $p \le 0.05$ (*corrected*) unless otherwise noted.

2.2. Effect of facial expression

A linear contrast of the regression coefficients was performed in order to identify voxels that demonstrated a greater response to faces displaying an emotional expression than to those displaying a neutral expression with direct-gaze. This contrast revealed voxel clusters in the bilateral STS, the right inferior frontal gyrus, and the bilateral occipital lobe that showed a stronger response to facial expressions (see Table 1 and Fig. 2). There were no clusters that showed a stronger response to neutral faces with direct-gaze.

2.3. Effect of averted-gaze

A linear contrast of the regression coefficients was performed in order to identify voxels that demonstrated a greater response to neutral faces with averted-gaze than to those with direct-gaze. This contrast revealed a cluster of voxels in the

Table 1
Brain regions with stronger responses to faces displaying an emotional expression than to those displaying a neutral expression ($p < 0.05$, corrected, $N = 12$)

Region	Maximum t-value	Volume (mm³)	x	y	z
Right middle occipital gyrus[a]	12.30	7507	32	−77	0
Left lingual gyrus[a]	8.08	7434	−17	−85	3
Right inferior frontal gyrus	9.50	6373	45	16	22
Right superior temporal sulcus	8.80	5907	52	−48	8
Left superior temporal sulcus	7.99	4539	−55	−60	10

[a] Cluster includes the inferior occipital gyrus and extends into the lateral fusiform gyrus.

Table 2
Brain region with stronger responses to faces displaying an averted-gaze than to those displaying a direct-gaze ($p < 0.05$, corrected, $N = 12$)

Region	Maximum t-value	Volume (mm³)	x	y	z
Right superior temporal sulcus	9.37	1878	36	−54	15

right STS region (see Table 2 and Fig. 2) that showed a stronger response to averted-gaze. There were no clusters that showed a stronger response to direct-gaze than to averted-gaze.

2.4. Expression > averted-gaze

A linear contrast of the regression coefficients was performed in order to identify voxels that demonstrated a greater response to faces displaying an emotional expression (direct-gaze) than to faces displaying an averted-gaze (neutral expression). This contrast revealed two large bilateral occipito-temporal clusters that showed a greater response to facial expressions. These clusters include the inferior occipital gyrus and extended bilaterally into the lateral fusiform gyrus (Table 3). There were no clusters that showed a stronger response to averted-gaze than to facial expression.

2.5. Response selectivity maps

A response selectivity map was created in order to compare the conjunction of regions that demonstrated significant activation for expression > control and/or averted-gaze > control. The map shows voxels that have one of three response profiles; greater response to expression than control; greater response to averted-gaze than to control; greater response to expression than to control *and* to averted-gaze than to control. These voxels clustered into three distinct overlapping regions in the right STS (see Fig. 2). Those voxels most sensitive to expression formed a region inferior and anterior to those most sensitive to averted-gaze,
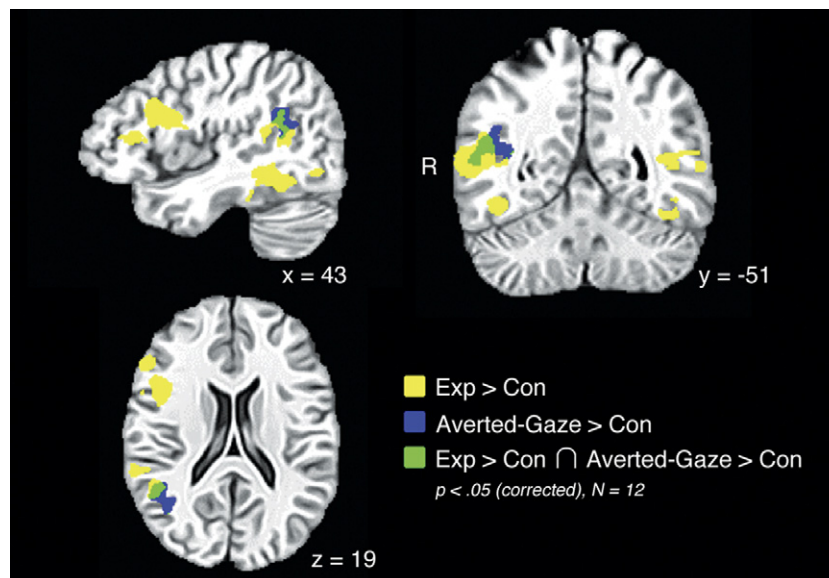

Fig. 2. Brain activity overlaid on a standardized brain. *Yellow* indicates voxels that showed a greater response to facial expressions than to control stimuli (neutral faces with direct-gaze). *Blue* indicates voxels that showed a greater response to faces with averted-gaze than to control stimuli. *Green* indicates voxels that showed a greater response to facial expressions than to control *and* a greater response to averted-gaze than to control.

Table 3
Brain region with stronger responses to faces displaying an emotional expression and direct-gaze than to those displaying a neutral expression and averted-gaze ($p < 0.05$, corrected, $N = 12$)

Region	Maximum t-value	Volume (mm³)	x	y	z
Right cuneus/middle occipital/fusiform gyri	13.67	22,020	43	−58	−4
Left cuneus/middle occipital/fusiform gyri	10.43	18,717	−21	−91	3

with those most sensitive to both occupying the space between.

The functional dissociation of these regions was noted across individual subjects as well as at the group level. Indeed, one subject did not have a single voxel with a significant effect for both the expression > control and averted-gaze > control contrasts. The spatial pattern of expression sensitive and averted-gaze sensitive voxels along the *S–I* axis in the group analysis also was largely evident in individual subjects, as the averted-gaze region was superior to the expression region in 10 of 12 (Supplementary Fig. S3).

2.6. Time-course analysis

The time-course analysis (Fig. 3) illustrates the response profile of the regions identified by the selectivity maps (Fig. 2). Notably, the expression-selective voxels in the STS responded significantly to all face conditions as compared to baseline.
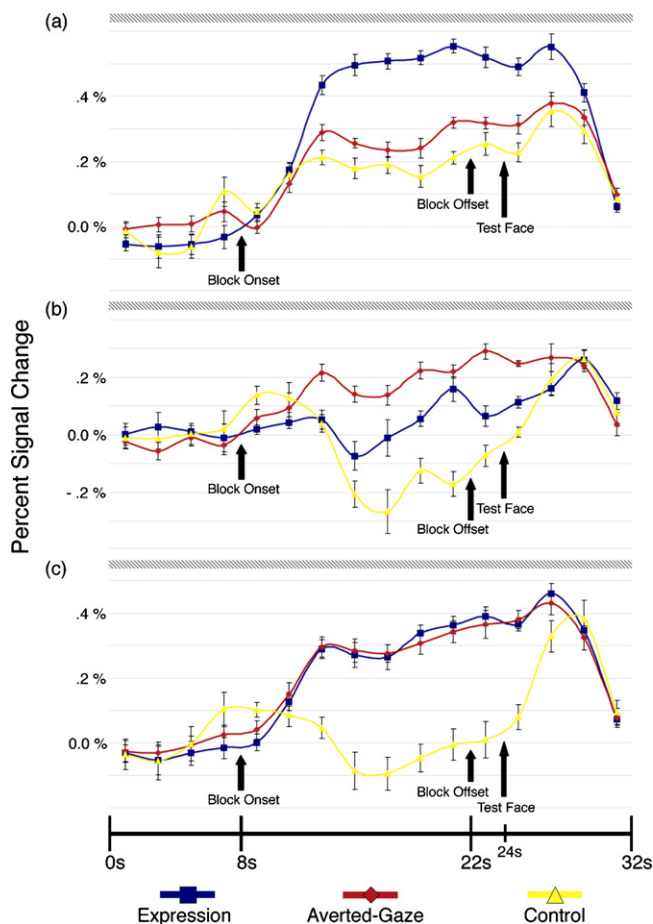

Fig. 3. The mean time series averaged across voxels within regions of interest: (a) mean response of voxels within posterior right STS that show a greater response to facial expressions that to control stimuli (neutral faces with direct-gaze), (b) mean response of voxels within posterior right STS that show a greater response to faces with averted-gaze than to control stimuli, (c) mean response of voxels within posterior right STS that show a greater response to facial expressions than to control *and* a greater response to averted-gaze than to control. The time series begins 8 s prior to the beginning of the stimulation stimulus block and terminates 8 s after presentation of the test face.

These time courses also reveal a clear increase in the hemodynamic response evoked by the test face across all conditions and regions of interest.

Within the face-responsive region of right ventral temporal cortex, perception of emotionally expressive faces elicited a significantly stronger response than averted-gaze faces ($p < 0.01$). The signal evoked by expressive faces also was greater than the signal evoked by control faces ($p = 0.02$). Conversely, the signal evoked by averted-gaze faces was less than the signal evoked by control faces ($p = 0.06$). These differences were most prominent in separate regions of the time course. Expression was most significantly different from control in the late half of the block (TRs 6–9; $p = 0.00003$) whereas averted-gaze was significantly less than control in the early part of the block (TRs 4–5; $p = 0.02$).

3. Discussion

This study supports our hypothesis that the STS region of human cortex contains dissociable representations for the perception of facial expression and averted-gaze. The hemodynamic response to faces in this region was significantly modulated by both the perception of expression and by the perception of averted-gaze. However, an inspection of the activity within this area revealed distinct, though overlapping, clusters of voxels that preferred facial expressions, averted-gaze, or both. Furthermore, our data strongly suggests that this functional dissociation adheres to a spatial pattern in which expression-selective voxels are located within the STS inferior to averted-gaze selective voxels.

This functional dissociation in normal human participants is consistent with neuropsychological evidence that gaze-perception deficits do not necessarily accompany expression perception deficits in patients with prosopagnosia (Campbell, Heywood, Cowey, Regard, & Landis, 1990). To the best of our knowledge however, there are no reported cases of patients with compromised gaze-perception and spared expression perception.

It is possible that the voxels in the current study that are modulated by facial gesture, irrespective of type, are responding to the implied motion inherent in static images of facial expression and averted-gaze direction. Previous studies have shown that perception of static images that imply motion will activate motion-selective areas of the STS (e.g. Kourtzi & Kanwisher, 2001; Senior et al., 2000). The posterior region of STS that responds to biological but not non-biological motion (Grossman & Blake, 2002) may be responding to both types of facial gesture presented in our study, but not to the control faces, which have less implied motion.

The overlap between the selective regions might, in part, represent an area responsible for the integration of expression and gaze-direction information. As noted earlier, a number of studies have found the perception of facial expression and gaze-direction to be behaviorally interdependent (e.g. Adams & Kleck, 2003, 2005; Ganel et al., 2005; Holmes et al., 2006; Hori et al., 2005; Mathews et al., 2003; Putman et al., 2006). Holmes et al. (2006) suggested that the behavioral integration noted in their study might be due to "interactions taking place

within STS and surrounding temporal areas". However, it was beyond the scope of this study to investigate the complex interactions between expression and gaze as the practical constraints of fMRI precluded us from fully crossing all factors (a fully crossed design would have included 25 conditions).

Interestingly, the voxels that strongly prefer expression in the right STS also evidence a significant response to neutral faces with direct or averted-gaze (see Fig. 3a). That is, all face conditions elicited a significant response, but the expression condition was significantly greater than both the averted-gaze and control conditions. This may be due to non-expression-selective cells interspersed within the more abundant expression-selective cells. The response selectivity of voxels could accurately represent the selectivity of the underlying cell population or the average of highly selective smaller populations. High resolution imaging of this region will be necessary to disambiguate these possibilities (Grill-Spector, Sayres, & Ress, 2006).

The perception of facial expression modulated the hemodynamic response in other "core" regions of the distributed face-processing network significantly more than the perception of averted-gaze. Specifically, the inferior occipital and fusiform gyri both responded more to emotional faces with direct-gaze than to control or averted-gaze faces. This likely reflects attentional-modulation rather than emotion-selectivity *per se*. Observing a facial display of emotion captures attention and focuses it on the face (Vuilleumier & Schwartz, 2001). The response to faces in the fusiform gyrus is strongly modulated by attention (Furey et al., 2006; Haxby et al., 1994; Vuilleumier, Armony, Driver, & Dolan, 2001; Wojciulik, Kanwisher, & Driver, 1998).

In contrast to the attentional capture of an emotional face, the perception of an averted-gaze causes a reflexive orientation of attention away from the face toward the target location of the gaze (e.g. Driver et al., 1999; Friesen et al., 1998; Hietanen, 1999; Langton & Bruce, 1999). This reflexive orientation can be overt or covert (Mansfield, Farroni, & Johnson, 2003) and will occur even when it jeopardizes task performance (Driver et al., 1999). Subjects in our study were, therefore, likely to have reflexively shifted attention to the periphery when viewing faces with an averted-gaze. Inspection of the time course from face-responsive ventral temporal voxels shows that, consistent with an attentional account, perception of averted-gaze initially reduces the response to faces in the fusiform cortex, as compared to the response to control faces. This effect diminishes over time. The transient nature of this effect suggests that the subjects habituate to the attentional effect of static images of averted-gaze.

Facial expressions also elicited a greater hemodynamic response than neutral faces in lateral areas of the right frontal lobe associated with motor control and an action/observation network. Cells in area F5 of the macaque have been shown to respond to execution and observation of the same action (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Our current investigation yielded a large cluster of activity along the right inferior frontal gyrus, the human homologue of F5 (Petrides & Pandya, 2002). Activation in this region has been previously noted during tasks involving the judgment of facial expressions (Carr et al., 2003; George et

al., 1993; Montgomery, Seeherman, & Haxby, 2006; Nakamura et al., 1999; Sprengelmeyer, Rausch, Eysel, & Przuntek, 1998). Nakamura et al. (1999) proposed that this activity most likely represents the engagement of the human mirror neuron system. Consistent with this explanation, electromyographic evidence shows that humans automatically imitate observed facial expressions (Dimberg & Thunberg, 1998; Dimberg, Thunberg, & Grunedal, 2002). The current study offers further evidence that simple perception of static facial expressions engages the frontal mirror neuron region.

One limitation of the current results is the omission of expressions of sadness and joy. Though it would have been ideal to include all six basic emotional expressions, the practical constraints of fMRI (e.g. low power and signal-to-noise ratio) precluded us from doing so. It is possible, therefore, that the current results do not generalize to all facial expressions.

3.1. Conclusion

This study is the first to demonstrate that the perception of two types of facial gesture, emotional expression and averted-gaze, are subserved by dissociable neural systems. We propose that within the right superior temporal sulcus distinct, though overlapping, regions of cortex support the perception of facial expressions and of gaze-direction.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuropsychologia.2007.06.022.

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