

Research Article

When Strangers Pass

Processing of Mutual and Averted Social Gaze in the Superior Temporal Sulcus

Kevin A. Pelphrey,^{1,2} Ronald J. Viola,¹ and Gregory McCarthy^{1,3}

¹Duke-UNC Brain Imaging and Analysis Center, Duke University Medical Center; ²Neurodevelopmental Disorders Research Center, Department of Psychiatry, The University of North Carolina at Chapel Hill, School of Medicine; and ³Department of Veterans Affairs Medical Center, Durham, North Carolina

ABSTRACT—Using functional magnetic resonance imaging (fMRI), we investigated brain activity evoked by mutual and averted gaze in a compelling and commonly experienced social encounter. Through virtual-reality goggles, subjects viewed a man who walked toward them and shifted his neutral gaze either toward (mutual gaze) or away (averted gaze) from them. Robust activity was evoked in the superior temporal sulcus (STS) and fusiform gyrus (FFG). For both conditions, STS activity was strongly right lateralized. Mutual gaze evoked greater activity in the STS than did averted gaze, whereas the FFG responded equivalently to mutual and averted gaze. Thus, we show that the STS is involved in processing social information conveyed by shifts in gaze within an overtly social context. This study extends understanding of the role of the STS in social cognition and social perception by demonstrating that it is highly sensitive to the context in which a human action occurs.

Gaze is a potent social cue, with mutual gaze often signaling threat or approach and averted gaze conveying submission or avoidance (Argyle & Cook, 1976; Baron-Cohen, 1995; Darwin, 1872/1965; Emery, 2000; Kleinke, 1986; Strongman & Champness, 1968). Processing of eye gaze is fundamental to social interactions, as demonstrated by its early emergence in ontogeny and disruption in autism (Hood, Willen, & Driver, 1998; Pelphrey et al., 2002). An explication of the neural substrate for gaze processing is an important step in the development of a neuroscience for social cognition.

There is general agreement that the superior temporal sulcus (STS) region is involved in the perception of eye gaze (Hoffman & Haxby, 2000; Pelphrey, Singerman, Allison, & McCarthy, 2003; Puce, Allison, Bentin, Gore, & McCarthy, 1998; Puce, Smith, & Allison, 2000; Wicker, Michel, Henaff, & Decety, 1998), and recent evidence suggests that this region is sensitive to the social context in which a gaze

shift occurs (Pelphrey, Singerman, et al., 2003). Thus, it might be expected that the degree to which the gaze of another person engages the observer would influence STS processing; however, neuroimaging studies that have compared mutual and averted gaze have reported conflicting findings (George, Driver, & Dolan, 2001; Hoffman & Haxby, 2000; Kawashima et al., 1999; Wicker et al., 1998). One functional magnetic resonance imaging (fMRI) study reported increased STS activity for averted compared with mutual gaze and an absence of differential activity in the fusiform gyrus (FFG; Hoffman & Haxby, 2000), whereas another reported increased activity in the FFG for mutual gaze compared with averted gaze and an absence of differential STS activity (George et al., 2001). A third fMRI study showed bilateral amygdala activity for mutual but not averted gaze (Kawashima et al., 1999). Finally, a positron emission tomography (PET) study reported equivalent STS activity for mutual and averted gaze (Wicker et al., 1998).

Three of the four aforementioned studies used static faces displaying mutual or averted gaze rather than dynamic faces in which the eyes shifted gaze from a neutral point to a state of mutual or averted gaze (George et al., 2001; Hoffman & Haxby, 2000; Wicker et al., 1998). Interpreting their findings is thus more challenging because differential activity may simply reflect differential quantities of motion implied by faces with averted gaze compared with mutual gaze (Kourtzi & Kanwisher, 2000; Senior et al., 2000). Moreover, previous studies have not examined mutual and averted gaze within realistic social contexts, but rather have presented isolated posed faces as stimuli. Hence, a central question remains concerning whether (and how) the STS and other brain regions are involved in processing the social information conveyed by mutual and averted gaze in compelling and socially demanding contexts.

In an early fMRI study, our laboratory first demonstrated the role of the STS in gaze processing (Puce et al., 1998), and we subsequently demonstrated that this region is sensitive to the intentionality of observed gaze shifts (Pelphrey, Singerman, et al., 2003). Here, using fMRI, we examined whether the STS participates in the visual analysis of social information conveyed by gaze shifts in an overtly social encounter that most readers will find familiar—a stranger walking past them in a hallway. Subjects viewed an animated male figure that

Address correspondence to Gregory McCarthy, Duke-UNC Brain Imaging and Analysis Center, Duke University Medical Center, 163 Bell Building, P.O. Box 3918, Durham, NC 27710; e-mail: gregory.mccarthy@duke.edu.



Fig. 1. Experimental conditions. The first 5.8 s of the 7.0-s walking sequence were identical for the two conditions (upper two panels, left to right). In mutual gaze (lower left), the figure's eyes moved toward the subject 5.8 s into the sequence. In averted gaze (lower right), the figure's eyes moved away from the subject 5.8 s into the sequence. The conditions were created using virtual-reality software to portray a commonly encountered social setting—a stranger passing in the hallway.

walked toward them and shifted his neutral gaze either toward (mutual gaze) or away (averted gaze) from them (see Fig. 1). We randomly changed the side from which the figure passed the observer, so that the identical gaze shift could serve for both mutual and averted gaze and thus control for any physical differences in the evoking stimulus. We reasoned that if gaze-related STS activity reflects the operation of a simple eye movement detector (or, more generally, a biological motion detector), the region should not respond differentially to mutual and averted gaze.

We found that mutual gaze evoked greater activity in the STS than did averted gaze. In contrast, the FFG responded equivalently to mutual and averted gaze. Thus, we show that the STS is involved in processing social information conveyed by shifts in gaze within an overtly social and dynamic context, and that activity in this region is influenced by the social context (that of approach or avoidance) in which an observed human action occurs.

METHOD

Subjects and Tasks

Eight right-handed healthy young adults (5 males) served as subjects for the fMRI task, and 6 more healthy young adults (3 males) participated in the behavioral task that was conducted outside of the scanner. All subjects provided written informed consent.

fMRI Task

Two experimental conditions were generated using the Poser 4.0[®] software program (Curious Labs Inc., Santa Cruz, California). In each,

subjects viewed a virtual hallway into which an animated male figure entered by rounding a corner on the far side; the figure walked toward them and shifted his eye gaze while passing, at exactly 5.8 s after the onset of the sequence (see Fig. 1). In the mutual-gaze condition (see the lower left panel of Fig. 1), the figure's eyes moved toward the subject, where they remained fixed for 1 s before exiting from view. In the averted-gaze condition (see the lower right panel of Fig. 1), the figure's eyes made a movement of equal magnitude and duration away from the subject before exiting from view. Prior to the gaze shift, the two conditions were identical.

On each trial, the figure entered from either the left or the right and appeared to pass by the observer on the left or right, respectively. We formed four possible stimulus configurations by crossing the direction of gaze with the side on which the figure passed the observer. Thus, averted gaze occurred when the figure moved his eyes to the right while passing on the right or moved his eyes to the left when passing on the left. Mutual gaze occurred when the figure moved his eyes to the right while passing on the left or moved his eyes to the left while passing on the right. Stimuli were counterbalanced so that the figure approached and passed the viewer from the left and right sides of the hallway an equal number of times. We emphasize that the mechanical aspects of the gaze shifts were identical across conditions. Only the direction of gaze, and the associated social signal, differed.

The program CIGAL (Voyvodice, 1999) was used to present stimuli at XGA resolution via LCD display goggles. Subjects were instructed to pay attention to the figure's eyes as he walked down the hallway. Each vignette lasted 7 s, and trials were separated by a 14-s intertrial interval (ITI), during which the subject viewed the hallway with no figure present. Trials were randomized within 7.25-min runs, and each subject completed an average of 8.5 runs.

Behavioral Task

The behavioral task included the same two conditions, as well as a third condition in which the passing figure did not make a gaze shift. Again, subjects viewed brief videos, which were separated by a 3- to 5-s ITI. Stimuli were presented on a 21-in. monitor at a comfortable seating distance, and subjects pressed buttons to indicate whether the figure looked toward or away from them. Subjects were instructed to make no response if they did not think the eyes shifted. Across 192 trials, each of the three conditions (mutual gaze, averted gaze, or no gaze) appeared 64 times in random order. Trials were presented in four runs lasting 8.87 min each (48 trials per run), and were again counterbalanced so that the figure approached from each side of the hallway an equal number of times.

Imaging and Data Analysis

For scanning, we used a General Electric 4-T LX NVi MRI scanner system equipped with 41-mT/m gradients and a quadrature birdcage radio frequency (RF) head coil for transmitting and receiving (General Electric, Milwaukee, Wisconsin). Sixty-eight axial images were acquired using a three-dimensional fast spoiled gradient-recalled echo pulse sequence (repetition time = 500 ms; echo time = 20 ms; field of view = 24 cm; image matrix = 256²; voxel size = 0.9375 × 0.9375 × 1.9 mm) and were used for co-registration with the functional data. Functional images were acquired using a gradient-recalled inward-spiral pulse sequence (Glover & Law, 2001) sensitive to blood-oxygenation-level-dependent (BOLD) contrast (repetition time = 1,500 ms; echo time = 35 ms; field of view = 24 cm; image matrix =

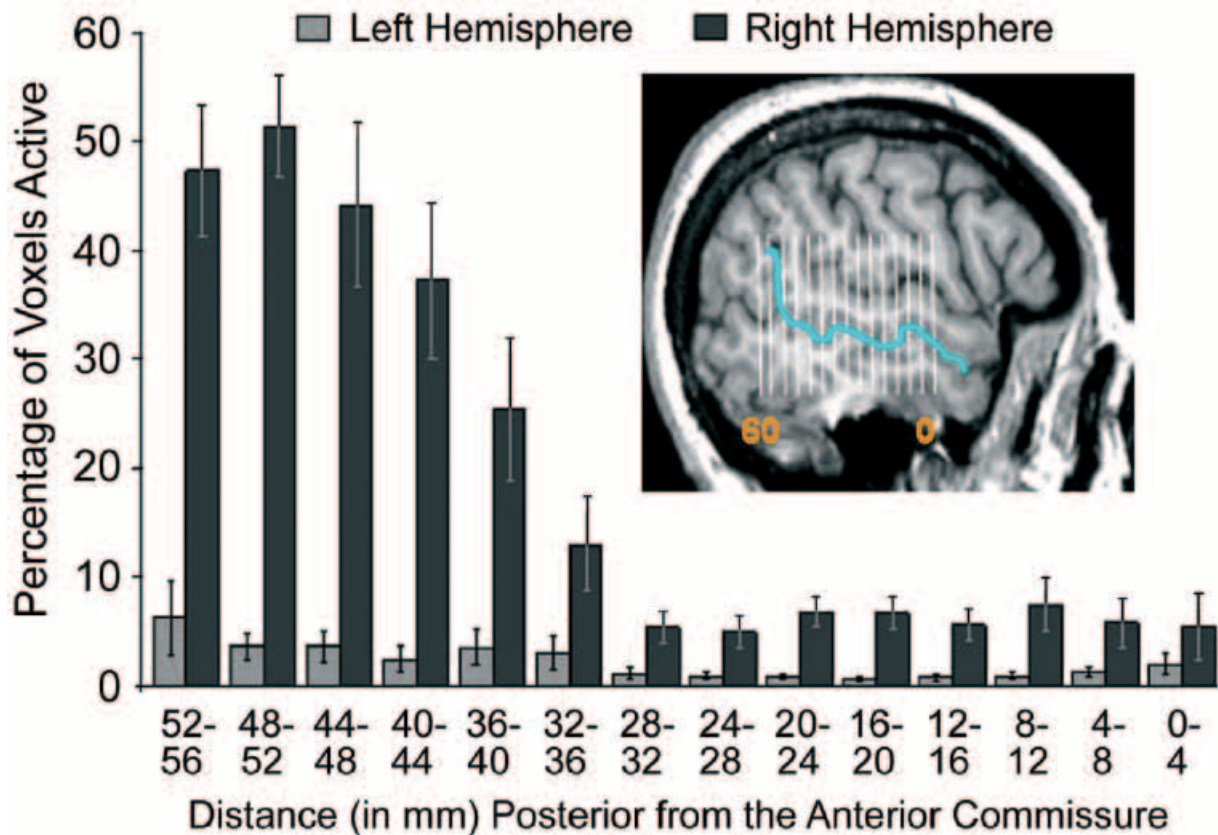


Fig. 2. Anterior-to-posterior distributions of activated voxels by hemisphere in the superior temporal sulcus (STS). As shown in the inset, the STS from each subject was divided into segments, with the first segment from each subject anchored at the anterior commissure. The inset illustrates how the STS region of interest was examined on a slice-by-slice basis.

64²; $\alpha = 62^\circ$; voxel size = $3.75 \times 3.75 \times 3.8$ mm; 34 axial slices). These parameters allowed whole-brain coverage. A semi-automated high-order shimming program ensured global field homogeneity. Runs consisted of 286 time points and began with four discarded RF excitations to allow for steady-state equilibrium.

Image preprocessing was performed using SPM 99 (Wellcome Department of Cognitive Neurology, Queen Square, London, United Kingdom). Motion was detected by center-of-mass measurements, and the data of 3 subjects were discarded prior to statistical analysis because of head motion greater than 4 mm. Functional images were temporally adjusted for interleaved slice acquisition and realigned to the 10th image to correct for head movements between scans. The realigned scans were co-registered to the subject's anatomic scan.

Our primary analytical approach consisted of an anatomic region-of-interest (ROI) analysis that had been used successfully in prior studies from our laboratory (Jha & McCarthy, 2000; Pelphrey, Mitchell, et al., 2003; Pelphrey, Singerman, et al., 2003; Wright, Pelphrey, Allison, McKeown, & McCarthy, 2003; Yamasaki, LaBar, & McCarthy, 2002). ROIs were traced on the left and right STS, FFG, and amygdala, using each subject's high-resolution anatomic images and aided by human brain atlases (Duvernoy, 1999; Mai, Assheuer, & Paxinos, 1997; Roberts, Hanaway, & Morest, 1987). Anatomically defined ROIs offer several advantages, including the ability to observe the average activity within a given area without making a priori assumptions about the shape or timing of the response. However, many voxels within an anatomically defined ROI may not be activated by a given task or

stimulus. Thus, the mean activity measured within the ROI may represent a dilution of the activity in a subset of interesting voxels.

To address this issue, we next conducted a correlational analysis with a theoretically defined reference waveform to identify subsets of activated voxels within each ROI. We specified a waveform that increased after the initial appearance of the walking figure and incorporated a second rise and peak coincident with the onset of the gaze shift. This allowed us to identify voxels that were sensitive to walking (the initial rise) and gaze shifts (the second increase). On a subject-by-subject basis, we correlated the 21-s time course of raw signal change from each voxel with this reference waveform and calculated *t* statistics for the correlation coefficients. We chose a relatively low significance threshold for the correlation of the template waveform with each voxel's average time series, $t(1, 16) > 1.96$, $p < .05$ (uncorrected), to allow for some shape variation. Thus, for each ROI in each subject, we identified sets of voxels that showed significant activation to biological motion, and we used these voxels in subsequent analyses. We converted the count of activated voxels within each ROI to a percentage relative to the number of voxels in that ROI. We then computed for each ROI the across-subjects average percentage BOLD signal change from baseline for each time point and each experimental condition. Two-tailed paired-sample *t* tests were used for all comparisons. Cohen's *d* effect-size estimates were calculated for critical comparisons.

To visualize the activations by condition and to identify possible regions of activity outside of the anatomic ROIs, we performed

voxel-based analyses on the group-averaged data. A functional time-course volume (averaged across subjects) and a *t*-statistic activation map (also averaged across subjects) was computed for each condition. These averages were created by first spatially normalizing the data (e.g., the *t*-statistic maps) from the individual subjects to a template using SPM 99 and then averaging these normalized data across subjects using a fixed-effects analysis. Activated voxels were defined as those with suprathreshold *t* values, with the threshold for activation set at $t(1, 16) > 12$ ($p < 2.05 \times 10^{-09}$, two-tailed, uncorrected).

RESULTS

fMRI Results

The vignettes strongly activated the STS, and a greater percentage of voxels was activated in the right hemisphere ($M = 19\%$, $SE = 2\%$) than in the left hemisphere ($M = 2\%$, $SE = 0.7\%$) of the STS regardless of experimental condition, confirming right-hemisphere laterality for processing biological motion in the STS, $t(7) > 6.32$, $p < .0005$ (Pelphrey, Mitchell, et al., 2003; Pelphrey, Singerman, et al., 2003; Puce et al., 1998). Unlike the STS, the FFG showed significant proportions of voxels that were activated by both conditions in both hemispheres (right: $M = 23\%$, $SE = 4\%$; left: $M = 22\%$, $SE = 5\%$), and there was no effect of hemisphere. We examined the amygdala because a previous neuroimaging study (Kawashima et al.,

1999) had implicated this region in gaze processing. However, in the present study, fewer than 4% of voxels were activated in either hemisphere of the amygdala, and the activated voxels produced an average time course of BOLD signal change that was very noisy and nonsynchronous with the shift in eye gaze.

The STS ROI from each subject was divided into fourteen 4-mm segments, as shown in the image inset of Figure 2. The first segment from each subject was anchored at the anterior commissure (AC). ROI labels indicated the hemisphere and the distance (in 4-mm increments) from the AC, allowing us to examine anterior-to-posterior gradients in activity in the STS, as shown in the main body of Figure 2. Two features of this graph are particularly noteworthy. First, the right lateralization of gaze-shift-related activity is evident at every 4-mm increment. Second, the results are consistent with those of a previous report from our laboratory (Pelphrey, Singerman, et al., 2003) in that there was a striking anterior-to-posterior gradient in the percentage of voxels activated in the right-hemisphere STS, with the highest percentages of activated voxels occurring 32 to 56 mm from the AC. This region corresponds to the posterior portion of the main branch of the STS complex and its ascending limb.

To determine whether activated voxels responded differentially to mutual and averted gaze, we compared the average BOLD signal change waveforms from the activated voxels within the ROIs. The average time courses from the right hemisphere of the STS are given in Figure 3.

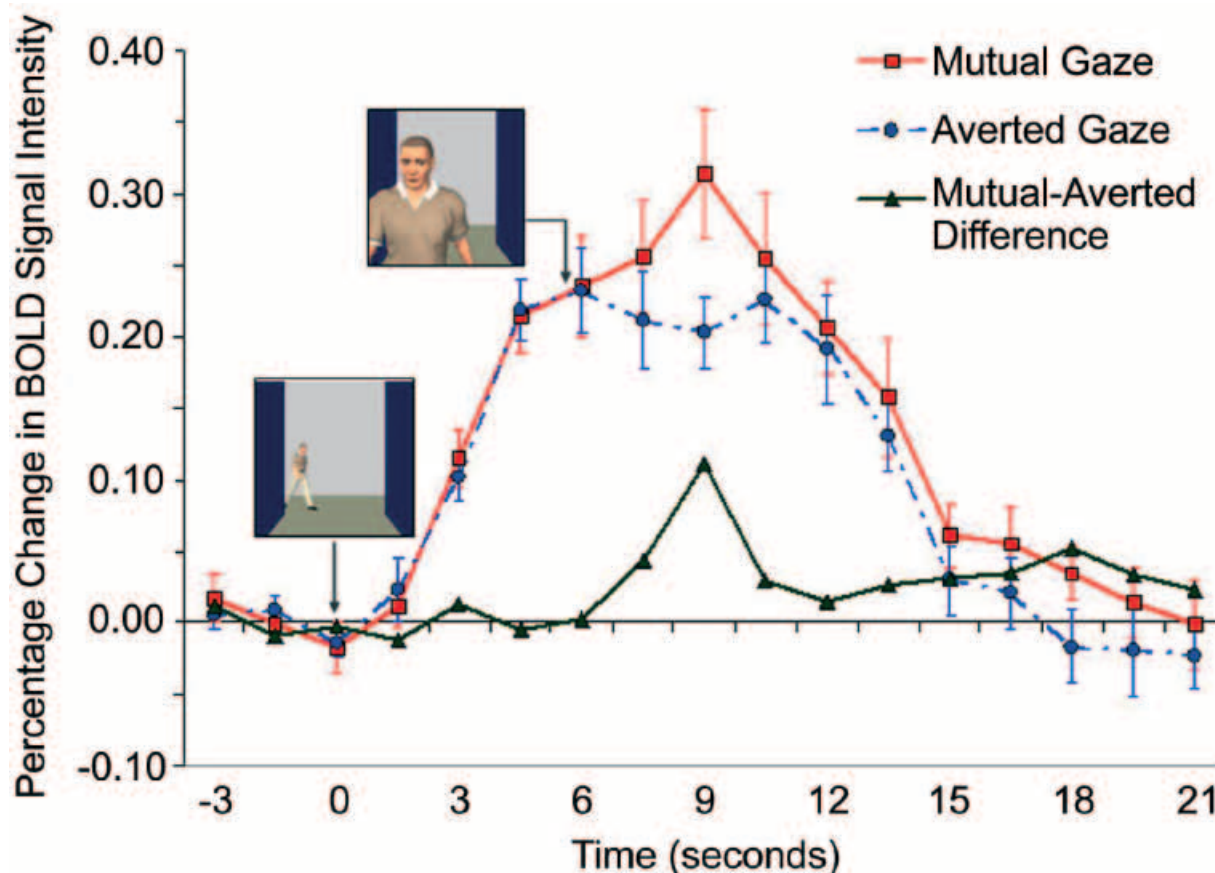


Fig. 3. Time courses of the average blood-oxygenation-level-dependent (BOLD) signal change from the activated voxels in the right-hemisphere superior temporal sulcus (STS). Responses in the mutual-gaze and averted-gaze conditions are plotted along with the difference waveform (mutual-gaze condition minus averted-gaze condition). The two still frames from the video mark the trial onset and the moment the gaze shift occurred.

The first 5.8 s of the waveforms should not have differed between conditions in any ROI because this segment of the walking sequence was identical in the two conditions. Additionally, the STS was expected to be activated during this segment because this region is known to be involved in processing observed biological motion, such as that conveyed by a walking person (Allison, Puce, & McCarthy, 2000; Pelphrey, Mitchell, et al., 2003). The data agreed with both of these expectations (see Fig. 3). However, in the mutual-gaze condition, at 5.8 s the figure's eyes moved toward the subject, where they remained fixed for 1 s before exiting from view. In the averted-gaze condition, the figure's eyes moved away from the subject at the same moment. Critically, in the right STS (Fig. 3), the two waveforms bifurcated shortly after this gaze shift, and the BOLD signal change was substantially greater for mutual gaze than for averted gaze. Thus, the change in BOLD signal was greater when subjects observed mutual gaze than when they observed averted gaze. In addition to the clear difference between mutual and averted gaze at 9 s, $t(7) = 3.43$, $p < .05$, Cohen's $d = 1.06$, smaller differences were observed late in the time courses (16.5 s to 19.5 s). The difference waveform (mutual gaze—averted gaze) shown in Figure 3 resembles a typical hemodynamic response, with a rise time-locked to the onset of the gaze shift and a peak 3 s after this shift. The pattern of effects for the small percentage of activated voxels in the left STS was identical to that reported here for the right STS.

In contrast to the STS, the FFG did not show differential activity for mutual versus averted gaze. Indeed, the time courses of BOLD percentage signal change from the left and right FFG completely overlapped.

As previously mentioned, the amygdala was not robustly activated by the stimuli used in the present study. Moreover, the small percentage (< 4%) of activated voxels produced average signal time courses that were very noisy and nonsynchronous with the shift in eye gaze.

The across-subjects t -statistic activation maps for the two conditions, displayed on a standard brain in Figure 4, illustrate the local-

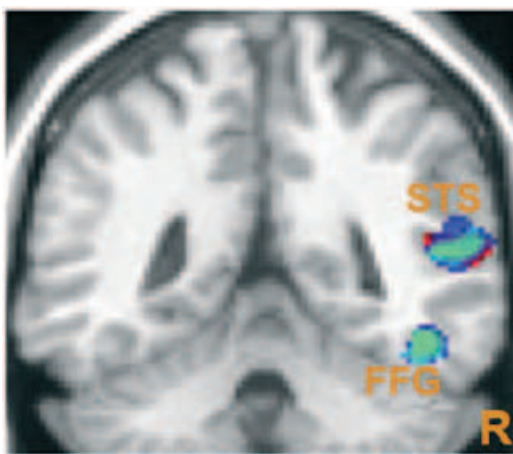


Fig. 4. Across-subjects t -statistic activation maps for the two conditions overlaid on a standard template brain. The red (mutual gaze) and blue (averted gaze) areas represent the magnitude (lighter shading = higher magnitude) of the voxel-by-voxel correlation between the reference waveform and the time course of the hemodynamic response for each condition. The averaged correlations were converted to t statistics with the threshold set at $t > 12$ ($p < 2.05 \times 10^{-09}$, two-tailed, uncorrected). At this threshold, completely overlapping activations were evoked by the two conditions in the right (R) superior temporal sulcus (STS) and fusiform gyrus (FFG).

ization of the activations reported here. The activation maps for mutual gaze and averted gaze were generally coextensive and were localized to the right STS and FFG. A third region (not shown) posterior and slightly inferior to the STS activation did not differentiate mutual and averted gaze and was likely the more general motion-sensitive region MT or V5 (MT/V5; McCarthy et al., 1995; Watson et al., 1993; Zeki, 1991).

Behavioral Results

To explore potential behavioral correlates of the effects observed in the fMRI task, we asked a different sample of subjects to view a modified version of the stimulus display and press buttons indicating whether the figure looked toward (mutual gaze) or away (averted gaze) from them. We introduced trials with no eye movement as foils. Accuracy did not differ between mutual gaze and averted gaze ($M_{\text{mutual}} = 97.60\%$ correct, $SE = 0.53$; $M_{\text{averted}} = 98.40\%$ correct, $SE = 0.70$), $t(5) = 1.53$, $p > .05$. However, subjects were significantly faster at responding to mutual gaze than averted gaze ($M_{\text{mutual}} = 726.70$ ms, $SE = 89$ ms; $M_{\text{averted}} = 764.90$ ms, $SE = 88$ ms), $t(5) = 4.30$, $p < .05$. These findings suggest that subjects devoted equal amounts of attention to the two stimulus conditions (as shown by equivalent levels of accuracy), but that some aspect of gaze processing was facilitated for mutual gaze relative to averted gaze (as revealed by the reaction time advantage for mutual gaze).

DISCUSSION

The fMRI results from the present study show that the STS is involved in processing the social information conveyed by shifts in eye gaze. In contrast to previous studies that focused on the role of the STS in processing static face stimuli (George et al., 2001; Hoffman & Haxby, 2000; Kawashima et al., 1999; Wicker et al., 1998), this study demonstrated that mutual gaze perceived within a dynamic, commonly encountered social setting evoked greater activity in the STS than did averted gaze perceived within the same social context. The differential response of the STS cannot be explained on the basis of discrepancies in the mechanical aspects of the two conditions because the eccentricity, velocity, and duration of the gaze shifts were equivalent. Only the direction of gaze differed, and we randomized the side of the figure's entry and exit.

Unlike in a previous neuroimaging study of gaze monitoring (Kawashima et al., 1999), the amygdala was not robustly activated in the present study. Given the proposed role of the amygdala in the analysis of facial expressions (McCarthy, 1999), it may not be surprising that we did not observe amygdala activity, as the figure in the vignettes displayed only a neutral expression. Future work might explore the amygdala response to various facial expressions (e.g., sadness, fear, happiness, disgust) displayed by the actor in socially realistic and meaningful vignettes like the one created here.

The FFG was engaged by aspects of the stimulus display—perhaps the presence of a face moving toward the subject—but responded equivalently to mutual and averted gaze. The absence of differential FFG activity in the current study provides added support for models of the human face-processing system that distinguish cortical regions involved in processing invariant characteristics of faces (i.e., characteristics that carry information about identity) from regions involved in processing dynamic aspects of faces (i.e., characteristics that

facilitate communication; Allison et al., 2000; Haxby, Hoffman, & Gobbini, 2000; McCarthy, 1999).

The present results complement previous findings from our laboratory concerning the sensitivity of the STS to the intention or goal directedness of a gaze shift (Pelphrey, Singerman, et al., 2003). In that study, as subjects viewed an animated face, a small checkerboard appeared and flickered in the character's visual field. On *correct* (goal-directed) trials, the character shifted its gaze toward the checkerboard, confirming the subject's expectation. On *incorrect* (non-goal-directed) trials, the character shifted its gaze toward empty space, violating the subject's expectation. "Errors" (incorrect trials) evoked a hemodynamic response with extended duration in the STS, thus indicating a strong effect of context.

If STS activation related to eye movement reflects a simple eye movement detector (or more generally, a biological motion detector), there should be no difference in activation for gaze shifts made to a visual target and identical gaze shifts made to empty space, nor (as in the present study) should there be differential activity for mutual versus averted gaze. The results of our previous study and the present findings provide converging evidence for the role of the STS in social perception and social cognition beyond the known role of this region in processing biological motion (Allison et al., 2000). Thus, we conclude that the human STS is involved in the visual analysis of social information conveyed by biological motions, including shifts in eye gaze, and that this region is sensitive to at least two aspects of the social context surrounding human actions: the intentionality of the action (Pelphrey, Singerman, et al., 2003) and, as shown here, the degree to which the action signals approach and avoidance.

Acknowledgments—This research was supported by the Department of Veterans Affairs and National Institute of Mental Health Grant MH-05286. Kevin Pelphrey was supported by National Institute of Child Health and Human Development Grant 1-T32-HD40127. Gregory McCarthy was supported by a Career Research Scientist award from the Department of Veterans Affairs. The authors thank Beau Mack and Allen Song for their assistance in stimulus development, data acquisition, data analysis, and manuscript preparation.

REFERENCES

- Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in Cognitive Sciences*, *4*, 267–278.
- Argyle, M., & Cook, M. (1976). *Gaze and mutual gaze*. New York: Cambridge University Press.
- Baron-Cohen, S. (1995). *Mindblindness: An essay on autism and "theory of mind"*. Cambridge, MA: MIT Press.
- Darwin, C. (1965). *The expression of the emotions in man and animals*. Chicago: University of Chicago Press. (Original work published 1872)
- Duvernoy, H.M. (1999). *The human brain: Surface, three-dimensional sectional anatomy with MRI, and blood supply*. New York: Springer-Wien.
- Emery, N.J. (2000). The eyes have it: The neuroethology, function and evolution of social gaze. *Neuroscience Biobehavioral Reviews*, *24*, 581–604.
- George, N., Driver, J., & Dolan, R. (2001). Seen gaze-direction modulates fusiform activity and its coupling with other brain areas during face processing. *NeuroImage*, *13*, 1102–1112.
- Glover, G.H., & Law, C.S. (2001). Spiral-in/out BOLD fMRI for increased SNR and reduced susceptibility artifacts. *Magnetic Resonance Imaging in Medicine*, *46*, 515–522.
- 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, E.A., & Haxby, J.V. (2000). Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nature Neuroscience*, *3*, 80–84.
- Hood, B.M., Willen, J.D., & Driver, J. (1998). Adult's eyes trigger shifts of visual attention in human infants. *Psychological Science*, *9*, 131–134.
- Jha, A., & McCarthy, G. (2000). The influence of memory load upon delay-interval activity in a working-memory task: An event-related functional MRI study. *Journal of Cognitive Neuroscience*, *12*, 90–105.
- Kawashima, R., Sugiura, M., Kato, T., Nakamura, A., Hatano, K., Ito, K., Fukuda, H., Kojima, S., & Nakamura, K. (1999). The human amygdala plays an important role in gaze monitoring: A PET study. *Brain*, *122*, 779–783.
- Kleinke, C.L. (1986). Gaze and eye contact: A research review. *Psychological Bulletin*, *100*, 78–100.
- Kourtzi, Z., & Kanwisher, N. (2000). Activation in human MT/MST by static images with implied motion. *Journal of Cognitive Neuroscience*, *12*, 48–55.
- Mai, J.K., Assheuer, J., & Paxinos, G. (1997). *Atlas of the human brain in section*. San Diego, CA: Academic Press.
- McCarthy, G. (1999). Physiological studies of face processing in humans. In M.S. Gazzaniga (Ed.), *The new cognitive neurosciences* (pp. 393–410). Cambridge, MA: MIT Press.
- McCarthy, G., Spicer, M., Adrignolo, A., Luby, M., Gore, J., & Allison, T. (1995). Brain activation associated with visual motion studied by functional magnetic resonance imaging in humans. *Human Brain Mapping*, *2*, 234–243.
- Pelphrey, K.A., Mitchell, T.V., McKeown, M.J., Goldstein, J., Allison, T., & McCarthy, G. (2003). Brain activity evoked by the perception of human walking: Controlling for meaningful coherent motion. *Journal of Neuroscience*, *23*, 6819–6825.
- Pelphrey, K.A., Sasson, N.J., Reznick, J.S., Paul, G., Goldman, B.D., & Piven, J. (2002). Visual scanning of faces in autism. *Journal of Autism and Developmental Disorders*, *32*, 249–261.
- Pelphrey, K.A., Singerman, J.D., Allison, T., & McCarthy, G. (2003). Brain activation evoked by perception of gaze shifts: The influence of context. *Neuropsychologia*, *41*, 156–170.
- Puce, A., Allison, T., Bentin, S., Gore, J.C., & McCarthy, G. (1998). Temporal cortex activation in humans viewing eye and mouth movements. *Journal of Neuroscience*, *18*, 2188–2199.
- Puce, A., Smith, A., & Allison, T. (2000). ERPs evoked by viewing facial movements. *Cognitive Neuropsychology*, *17*, 221–240.
- Roberts, M., Hanaway, J., & Morest, D.K. (1987). *Atlas of the human brain in section*. Philadelphia: Lea and Febiger.
- Senior, C., Barnes, J., Giampietro, V., Simmons, A., Bullmore, E.T., Brammer, M., & David, A.S. (2000). The functional neuroanatomy of implicit-motion perception or representational momentum. *Current Opinion in Biology*, *10*, 16–22.
- Strongman, K.T., & Champness, B.G. (1968). Dominance hierarchies and conflict in eye contact. *Acta Psychologica*, *28*, 376–386.
- Voyvodic, J.T. (1999). Real-time fMRI integrating paradigm control, physiology, behavior, and on-line statistical analysis. *NeuroImage*, *10*, 91–106.
- Watson, J.D., Myers, R., Frackowiak, R.S., Hajnal, J.V., Woods, R.P., Mazziotta, J.C., Shipp, S., & Zeki, S. (1993). Area V5 of the human brain: Evidence from a combined study using positron emission tomography and magnetic resonance imaging. *Cerebral Cortex*, *3*(2), 79–94.
- Wicker, B., Michel, F., Henaff, M.A., & Decety, J. (1998). Brain regions involved in the perception of gaze: A PET study. *NeuroImage*, *8*, 221–227.
- Wright, T.M., Pelphrey, K.A., Allison, T., McKeown, M.J., & McCarthy, G. (2003). Polysensory interactions along lateral temporal regions evoked by audiovisual speech. *Cerebral Cortex*, *13*, 1034–1043.
- Yamasaki, H., LaBar, K.S., & McCarthy, G. (2002). Dissociable prefrontal brain systems for attention and emotion. *Proceedings of the National Academy of Sciences, USA*, *99*, 11447–11451.
- Zeki, S. (1991). A direct demonstration of functional specialization in human visual cortex. *Journal of Neuroscience*, *11*, 641–649.

(RECEIVED 6/13/03; REVISION ACCEPTED 9/4/03)