Distinct representations of eye gaze and identity in the distributed human neural system for face perception

Elizabeth A. Hoffman and James V. Haxby

Section on Functional Brain Imaging, Laboratory of Brain and Cognition, National Institute of Mental Health, Building 10, Room 4C104, Bethesda, Maryland 20892-1366, USA

Correspondence should be addressed to E.A.H. (elizabeth_hoffman@nih.gov)

Face perception requires representation of invariant aspects that underlie identity recognition as well as representation of changeable aspects, such as eye gaze and expression, that facilitate social communication. Using functional magnetic resonance imaging (fMRI), we investigated the perception of face identity and eye gaze in the human brain. Perception of face identity was mediated more by regions in the inferior occipital and fusiform gyri, and perception of eye gaze was mediated more by regions in the superior temporal sulci. Eye-gaze perception also seemed to recruit the spatial cognition system in the intraparietal sulcus to encode the direction of another's gaze and to focus attention in that direction.

Whereas the invariant aspects of a face allow one to recognize who someone is, the changeable aspects of a face can be used to infer information about that person's state of mind. Most face viewing occurs in the context of social communication after identity has been established. One example of information gleaned from a face during social interaction is the direction of another's gaze, which can indicate where that person's attention is directed and can be used to similarly direct one's own attention.

Impaired face recognition (prosopagnosia) is associated with ventral temporal lesions[1–3]. Within ventral temporal cortex, neuroimaging studies of face perception identify a region in the lateral fusiform gyrus (LFG) that responds more to faces than to other objects[4–7]. It is unclear, however, whether the perceptual analysis of all aspects of faces is mediated by this region. Other regions that respond preferentially, but less consistently, to faces are identified in the lateral inferior occipital gyri (IOG) and in the posterior superior temporal sulcus (STS)[4,6,8]. The STS region is also associated with the perception of eye and mouth movement[9,10] and may be homologous to a region in the superior bank of the STS in the monkey in which cells respond preferentially to faces, eye-gaze direction and face expression[11–14]. We hypothesized that the human face-responsive region in the STS may also be more involved in the perception of changeable aspects of faces and that the human face-responsive region in the LFG may be more involved in the perception of face identity. We hypothesized further that perception of the direction of eye gaze would elicit activity in regions associated with spatial perception and spatially directed attention, namely the intraparietal sulcus (IPS).

We conducted two experiments to test these hypotheses. In our first experiment, we tested whether selective attention to identity and eye-gaze direction modulated activity differently in these brain regions (**Fig. 1**, upper panel). If the representation of identity were more dependent on activity in the LFG, then selective attention to identity should elicit a stronger response in that region than attention to eye-gaze direction. Similarly, if the representation of eye-gaze direction were more dependent on activity in the STS, then selective attention to gaze should elicit a stronger response in that region than attention to identity. In our second experiment, we examined the strength of responses elicited by passive viewing of faces in which gazes were averted as compared with viewing of faces in which gazes were direct (**Fig. 1**, lower panel). Given that the perception of averted gaze causes a seemingly reflexive attention shift[15], passive viewing of faces in which gazes are averted should elicit stronger responses in the IPS, a brain region associated with covert shifts of spatial attention[16–18], than viewing of faces in which gazes are direct.

RESULTS

Accuracy and response times were similar for selective attention to identity and eye gaze ($93 \pm 6.0\%$, mean $\pm$ s.d., versus $92 \pm 5.0\%$, n.s.; 686 ms ± 129 ms versus 722 ms ± 147 ms, n.s.), indicating that the tasks were well matched on difficulty and attentional demand.

Four bilateral regions that responded more to faces than to control stimuli (scrambled pictures) were identified, in the LFG, STS, IOG and IPS (**Table 1** and **Fig. 2**). Of the seven subjects who showed significant activations in the regions that were the subject of our experimental hypotheses, namely the LFG and the STS, bilateral LFG and IOG regions were identified in all subjects, STS regions were identified in all subjects on the right and in four subjects on the left, and IPS regions were identified in all subjects on the left and in five subjects on the right. As we had hypothesized, selective attention to face identity and eye gaze had opposite effects in the LFG and STS (region $\times$ attention interaction, $p < 0.001$ on both the right and left), demonstrating that these regions participate differentially in the representation of the invariant and changeable aspects of a face. In the LFG, attention to identity elicited a stronger response than did attention to gaze (1.21% versus 0.90%, $n = 7$, $p < 0.001$, on the right; 1.23% versus 0.95%, $n = 7$, $p < 0.001$, left). By contrast, in the STS, attention to gaze elicited a stronger response than did attention to identity on the left (0.74% versus 0.47%, $n = 4$, $p < 0.001$), with no significant difference in the same direction in the right STS (0.79% versus 0.72%, $n = 7$, n.s.). The
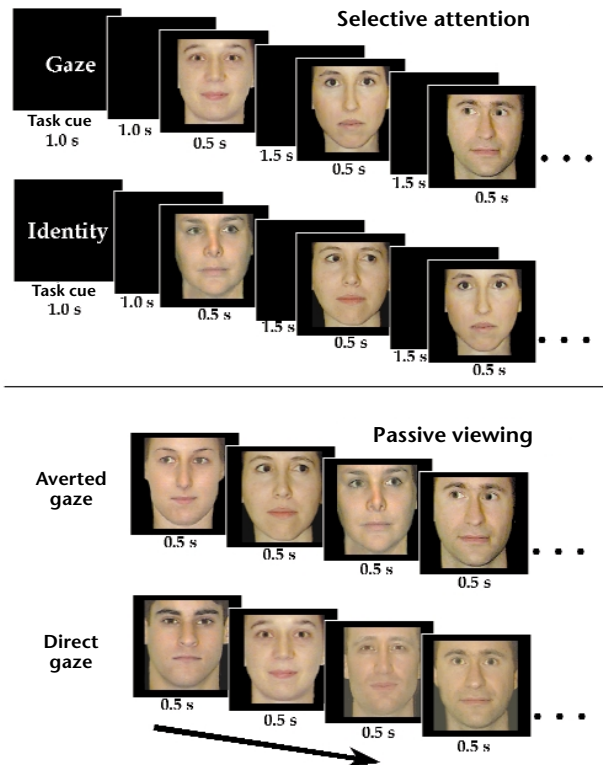
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Fig. 1. Face-perception tasks. The one-back repetition detection tasks in experiment 1 are displayed in the upper panel. Subjects attended selectively to the direction of eye gaze or the identity of each face. In the passive-viewing conditions in experiment 2 (lower panel), subjects viewed series of faces that either had the eyes all directed away from the viewer or all directed at the viewer.

left IPS than did attention to identity (0.99% versus 0.80%, $n = 7$, $p < 0.001$), with a nonsignificant difference in the same direction in the right IPS (0.88% versus 0.85%, $n = 5$, n.s.). Similar to the findings in the STS, the effects of task on responses in the right and left IPS did not differ significantly ($p > 0.1$).

The enhanced response in the IPS while attending to eye gaze suggested recruitment of the spatial cognition system. The direction of another's eye gaze is a potent cue for directing one's own spatial attention. Shifts of attention in response to the perception of averted gaze are observed in monkeys, apes and young infants[19–23], and are elicited in adults while fixating on a face, even when the direction of gaze is task-irrelevant[15], suggesting that our subjects also made covert, reflexive shifts of attention when the perceived gaze was averted.

It was also possible that the differential response in the IPS could be attributed to differences in the aperture of spatial attention. Presumably, the aperture of attention is narrower when attending to eye gaze than when attending to identity. To rule out this alternative explanation, we conducted a second experiment using two passive viewing conditions in which subjects were not instructed to attend to a specific facial feature. Subjects passively viewed faces that had averted gazes in one condition and passively viewed faces that had direct gazes in the other (**Fig. 1**, lower panel). The faces in each condition never repeated, so that the entire stimulus, not just the eye region in the averted gaze condition, varied from one trial to the next. Passive viewing of faces with averted gazes elicited significantly stronger responses than did passive viewing of faces with direct gazes in the IPS bilaterally (on the right, 0.35% versus 0.16%, $n = 5$, $p < 0.001$; on the left, 0.17% versus 0.06%, $n = 7$, $p < 0.05$) and in the left STS (0.39% versus 0.27%, $n = 4$, $p < 0.01$). By contrast, direction of gaze had no effect on the response to faces in the right STS or bilaterally in the IOG or LFG. The difference in the right STS, however, was in the same direction as in the left STS, and the sizes of this effect in the right and left did not differ significantly ($p > 0.1$).

DISCUSSION
The results of these experiments indicate that face identity and eye gaze have distinct representations within the distributed human neural system for face perception. This distributed system includes bilateral regions in the IOG, LFG and STS, all of which show a greater response to faces than to other objects[4,6,8,24]. Additionally, a region in the IPS was activated by our tasks,

effects of task on responses in the right and left STS did not differ significantly ($p > 0.1$). Additionally, we found that, as in the LFG, attention to identity elicited a stronger bilateral response in the IOG than did attention to gaze (on the right, 0.99% versus 0.85%, $n = 7$, $p < 0.005$; on the left, 1.10% versus 0.85%, $n = 7$, $p < 0.001$). As in the STS, attention to gaze elicited a stronger response in the

Table 1. Volumes and stereotaxic brain atlas coordinates[45] for the brain regions activated by viewing faces as compared to viewing scrambled pictures (mean ± s.d.).

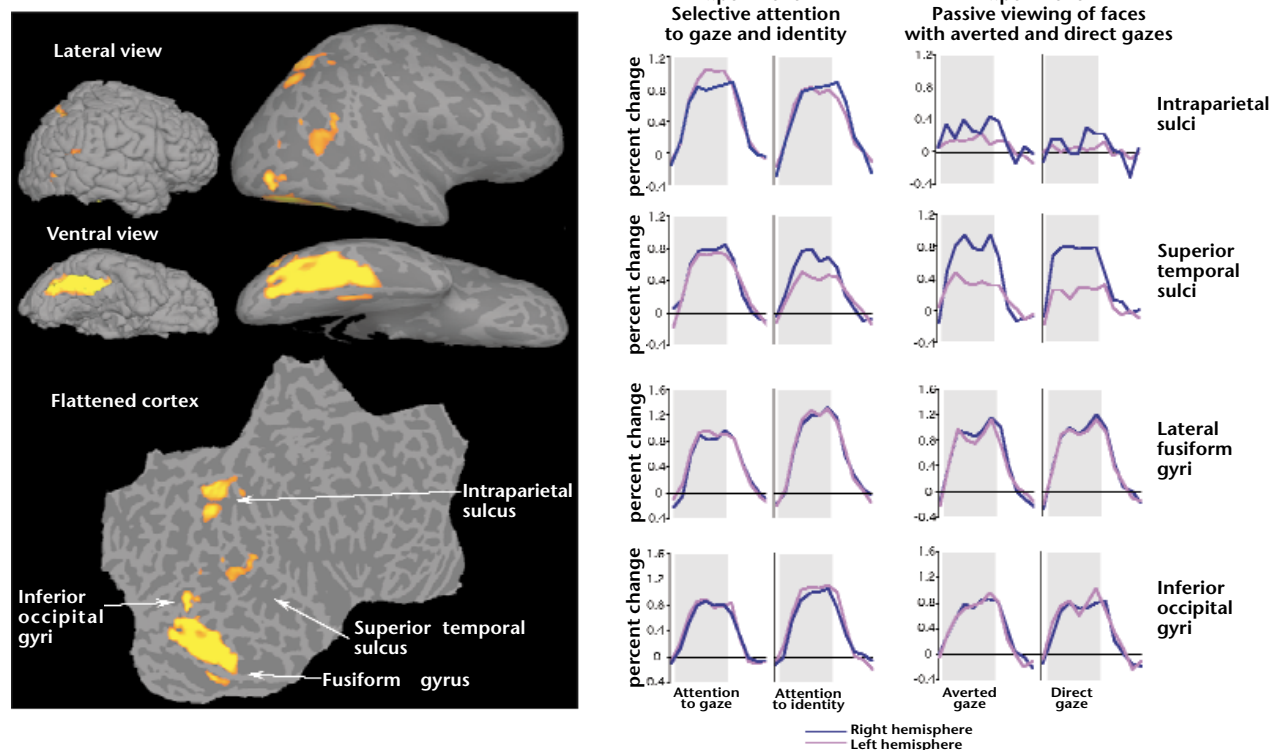| Region	Hemisphere	n	Volume (cm³)	Talairach coordinates (mm)		
				x	y	z
Fusiform gyrus	left	7	2.5 ± 0.7	−37 ± 1	−60 ± 1	−22 ± 4
	right	7	2.7 ± 0.6	39 ± 2	−55 ± 2	−22 ± 3
Superior temporal sulcus	left	4	1.8 ± 0.4	−45 ± 1	−56 ± 3	11 ± 2
	right	7	1.9 ± 0.6	50 ± 1	−63 ± 4	4 ± 7
Inferior occipital gyrus	left	7	2.5 ± 0.4	−31 ± 1	−82 ± 1	−15 ± 4
	right	7	2.2 ± 0.7	41 ± 2	−79 ± 3	−14 ± 5
Intraparietal sulcus	left	7	2.9 ± 0.6	−33 ± 2	−52 ± 3	45 ± 2
	right	5	2.7 ± 0.7	29 ± 3	−58 ± 4	50 ± 1

Fig. 2. fMRI results. The left panel shows regions activated by the face-perception tasks ($z > 4.0$) in the right hemisphere of one subject. Regions are shown on the folded surface, presented in lateral and ventral views (upper left figures) and on the cortical surface, inflated to show the extent of activated regions in the sulci. The lower figure shows the cortical surface for the entire right hemisphere presented as a flat, two-dimensional surface. Sulcal cortex obscured in the folded surface is shown with a darker shade of gray on the inflated and flattened surfaces. On the flattened cortex, occipital cortex is on the left and frontal cortex is on the right. The right panel shows mean time series in regions of interest, averaged across voxels in the regions, repetitions of task blocks and subjects. Gray bars indicate the presentation of task blocks. White spaces following task blocks indicate control task blocks that follow each task. See text for statistical comparisons.

although this region does not typically show selectivity for faces but, rather, is more typically associated with spatial perception and spatial attention[16–18,25].

The representation of face identity, which is based on aspects of facial structure that are invariant across changes in eye gaze or expression, is more dependent on activity in the IOG and LFG than on activity in the STS. In the monkey, neurons in the convexity of the inferior temporal (IT) gyrus show greater selectivity for different individual faces than do neurons in the STS[11], although some STS neurons also respond differentially to individual faces[12–14]. The human ventral temporal regions that are face-responsive may be homologous to the monkey IT region that is tuned to face identity. This conclusion is consistent with the literature on lesions that cause prosopagnosia[1–3,26]. Neuroimaging research on the role of the LFG has been ambiguous[27,28]. An early study showed that the fusiform gyrus was activated more when subjects attended to face identity than when they attended to gender[27]. Studies of the effect of face inversion on the activity in the LFG, however, generate doubt as to whether this region encodes face identity or simply the generic facial configuration[4,5,29]. Inversion impedes recognition of identity but has only a small and nonspecific effect on LFG activity. Our results clearly implicate the LFG in the perception of identity. The effect of face inversion suggests that LFG activity may reflect the attempt to perceive identity, not the successful generation of a distinct representation of an individual's face.

The representation of eye gaze, a changeable aspect of the face, depends more on activity in the STS than on activity in the IOG and LFG. Our results show that selective attention to gaze direction elicits a stronger response in the left STS than does attention to identity. An earlier neuroimaging study showed that perception of eye and mouth movement selectively activates the STS bilaterally[9]. An event-related potential (ERP) study with scalp electrodes using the same moving stimuli that evoked activity in the STS revealed that perception of averted gaze evokes a stronger N170 response than does perception of direct gaze[30], consistent with our results. Moreover, N200 responses measured with subdural electrodes placed on ventral face-specific sites do not differ significantly for perception of averted and direct gaze[31], consistent with our findings in the LFG in experiment 2. A positron emission tomography study showed STS activation during perception of averted and direct gaze[10], but no difference between these conditions, in contrast with our fMRI results and the scalp ERP results[30]. Our results indicate that the STS has a more general role in the perception of changeable aspects of faces, even when viewing static images. This conclusion is consistent with electrophysiological and lesion studies in monkeys. Monkey STS contains cells that respond differentially to gaze directions and facial expressions in static pictures[11–14]. These findings have led to the proposal that within face-responsive regions there are independent cell populations that perceive social signals from the face[12–14], and that these

cells are more prevalent in the STS than in IT cortex[11]. Lesions of monkey STS are associated with impaired perception of eye gaze with preservation of the perception of face identity[32,33]. Dissociation of impairments of face-identity recognition, on the one hand, from impairments of the perception of eye-gaze direction or facial expression, on the other, is reported in human lesion studies, but the anatomical locations of lesions that can cause selective impairment of eye-gaze perception are unclear[26,32].

Neuroimaging studies of other changeable aspects of faces also implicate the STS. In one study, perception of facial expression elicited a response in regions with coordinates close to our STS region[34]. In another study, lip reading also elicited a response in similar regions[35]. Together with our results, these findings and studies of monkey STS suggest that the STS may play a more general role in the representation of changeable aspects of the face.

Studies of the perception of face expression and lip-reading suggest that these operations also elicit activity in additional systems that process the significance of information gleaned from the face. Perception of fearful and disgusted facial expressions elicit further activity in limbic regions associated with processing emotion[34,36,37]. Lip-reading elicits further activity in regions associated with auditory processing of speech sounds[35].

Our results show that the perception of averted eye gaze elicits further activity in the spatial cognition system in the IPS. The IPS is activated during tasks involving spatial perception and covert shifts of spatial attention[16–18,25]. Presumably, the IPS was recruited in our tasks to encode the spatial direction of another's gaze and, additionally, perhaps, to mediate covert, reflexive shifts of spatial attention in that direction. The role played by the IPS in mediating covert shifts of spatial attention is presumably the same whether that shift is elicited by perceived eye gaze, as in our experiment, or by some other spatial cue.

An alternative account of the differential IPS response is that perception of averted gaze elicited eye movements that resulted in enhanced IPS activity. To rule out this explanation, we recorded eye movements using the ISCAN eye tracking system (Burlington, Massachusetts) while four different subjects performed the selective attention and passive viewing tasks outside the scanner. The mean number of saccadic eye movements was similar for selective attention to identity and eye gaze (18-s stimulus block; 29 ± 5 s, mean $\pm$ s.d., versus 28 ± 7 s, n.s.) and for passive viewing of direct and averted gaze (20 ± 7 s versus 18 ± 7 s, n.s.). Moreover, the horizontal and vertical amplitudes of eye movements did not differ for selective attention to identity versus eye gaze (horizontal, $1.6 \pm 0.4°$ versus $1.7 \pm 0.3°$, n.s.; vertical, $0.6 \pm 0.3°$ versus $0.4 \pm 0.2°$, n.s.) or for passive viewing of direct versus averted gaze (horizontal, $1.5 \pm 0.2°$ versus $1.3 \pm 0.3°$, n.s.; vertical, $0.6 \pm 0.5°$ versus $0.5 \pm 0.4°$, n.s.). Given these results, it is unlikely that the enhanced IPS activation in experiments 1 and 2 was due to greater eye movements during selective attention to gaze or passive viewing of averted gaze. These results also suggest that attention to identity, as compared to attention to eye gaze, did not result in significantly more scanning of the face or more eye movements with a vertical component. Therefore, it is unlikely that differential responses when attending to gaze and identity can be attributed to differences in the parts of the faces that were foveated during these tasks.

Behavioral studies indicate that monkeys and apes use gazes of others as cues to direct attention[19,23]. Human infants as young as three months shift attention in the direction of perceived gaze[21,22]. One study with adult subjects suggests that these shifts may be reflexive, occurring even when the direction of perceived gaze is task-irrelevant[15]. Reciprocal connections between cell populations in the superior bank of the STS and the IPS[38] could mediate

the transfer of information about social signals gleaned from the face, particularly those concerning direction of spatial attention[38]. Such connections in the human brain could mediate the recruitment of the IPS when the STS detects an averted gaze. One fMRI study showed that perception of lateral eye movement also activates the IPS[9], consistent with our contention that the IPS activity is specifically associated with the spatial aspects of perceived eye gaze and its role in directing attention.

Another fMRI study found that perception of direct gaze, but not averted gaze, elicits activity in the amygdala[39], but detected no face-responsive region in the STS, perhaps because the control task (opening and closing of the eyes) also involves perception of facial movement. The amygdala was not included in the volume we scanned. An amygdalar response may reflect the emotional significance of direct gaze, which is perceived as more socially engaging or potentially threatening than is averted gaze[40,41]. Monkeys respond more emotionally and make more appeasement gestures when gaze is directed at them than when gaze is directed away[42,43]. Connections between the STS and the amygdala may mediate processing of the emotional content of direct gaze.

Face perception can provide a wealth of information that facilitates social communication. There are two classes of face-perception operations that require independent representations. One class involves the perception of the changeable aspects of the face, such as expression and eye-gaze direction, whereas the other involves the perception of aspects of facial structure that are invariant across these changes. Perception of changeable aspects provides information about another person's current state of mind[44]. Eye gaze, in particular, is a powerful social signal that can guide our attention and can inform us about the intentions and interest of another person. Perception of invariant aspects of facial structure underlies the recognition of identity. Our results indicate that face perception is mediated in humans by a distributed system that comprises multiple regions, and that changeable and invariant aspects of faces have distinct representations within this system.

METHODS

Tasks. In experiment 1, subjects performed repetition-detection tasks that directed attention to identity or eye gaze. In each block of trials, nine faces were presented sequentially in the center of a screen for 0.5 s with an interstimulus interval of 1.5 s. At the beginning of each block of trials, a cue word ('identity' or 'gaze') was displayed for 1 s to inform the subject as to which task to perform. Subjects indicated whether the selectively attended aspect of each face matched that of the preceding face by pressing a button with the right (match) or left (nonmatch) thumb. In a control task, scrambled, nonsense, color images were presented at the same rate and in the same format as the stimuli in the repetition-detection tasks. In these trials, subjects pressed both the right and left buttons simultaneously when each stimulus appeared. Blocks of control trials alternated with repetition-detection blocks. In experiment 2, subjects passively viewed color faces that were blocked by gaze direction (laterally averted or direct). Subjects were instructed simply to look directly at each picture. Stimuli were presented sequentially at a rate of 2 per s in the center of the screen. Each block consisted of 36 stimuli. Face blocks alternated with control blocks during which nonsense stimuli were presented at the same rate and in the same format as were stimuli in the face blocks. The order of blocks in both experiments was counterbalanced across subjects and time series. Ten time series, each consisting of eight face blocks and nine control blocks, were obtained for each subject (six in experiment 1 and four in experiment 2).

Imaging. We scanned 9 healthy volunteers (3 male, 6 female, mean age, 24 ± 2.5 years). Each subject gave written informed consent and was compensated for participation. Our experimental protocol was approved by the institutional review board of the National Institute of Mental Health. Twenty contiguous, coronal, 5-mm thick slices were obtained in 10 time

series of 102 time points each (TR = 3 s). We used a gradient echo, echo planar imaging sequence (TE = 40 ms, FOV = 20 cm, 64 × 64 pixels per inch matrix, resolution, 3.125 × 3.125 × 5 mm) on a GE signa 1.5 Tesla magnet (General Electric, Milwaukee, Wisconsin).

Statistics. We registered our images using Automated Image Registration (AIR) provided by Roger Woods (Laboratory of Neuroimaging, UCLA). Following this, a 1.2-voxel smoothing filter was applied to each scan. We identified regions that showed a significant response to faces as compared to control stimuli in experiment 1; thus, these regions were defined independently of response differences between attention to identity and attention to gaze or between passively viewed direct gaze and averted gaze. Using multiple regression, we selected clusters of 7 or more contiguous voxels that showed a significant difference ($z > 4$) for the contrast between face and control blocks. The probability of finding a cluster of that size by chance was $p < 0.001$ in all subjects. Further analysis was restricted to the seven subjects who showed significant activations in the regions that were the subject of our experimental hypotheses, namely the fusiform gyrus and the STS. Brain atlas coordinates[45] for all regions were obtained using Statistical Parametric Mapping[46] (SPM96, Wellcome Department of Cognitive Neurology, London). Mean time series were calculated for each region, averaging across voxels and across repetitions of task blocks, in each subject, and were analyzed separately for experiments 1 and 2. The time series were extracted from regions activated by the face versus control comparison in experiment 1. These regions of activation were selected based on their responsiveness to faces generally and were therefore independent of our specific hypotheses in experiments 1 and 2. Multiple regression was used to measure the size of the response to each face task condition as a percent change above control. Multiple regression used two regressors of interest to contrast faces versus control and the two face-task conditions (experiment 1, identity versus gaze; experiment 2, averted gaze versus direct gaze). Measures of percent response were then analyzed with a repeated-measures analysis of variance with planned comparisons for the interaction between region (LFG versus STS) and face task (identity versus gaze) in experiment 1 and for the simple differences between face task conditions in both experiments in all regions.

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