



Commonalities in the neural mechanisms underlying automatic attentional shifts by gaze, gestures, and symbols

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ABSTRACT

Eye gaze, hand-pointing gestures, and arrows automatically trigger attentional shifts. Although it has been suggested that common neural mechanisms underlie these three types of attentional shifts, this issue remains unsettled. We measured brain activity using fMRI while participants observed directional and non-directional stimuli, including eyes, hands, and arrows, to investigate this issue. Conjunction analyses revealed that the posterior superior temporal sulcus (STS), the inferior parietal lobule, the inferior frontal gyrus, and the occipital cortices in the right hemisphere were more active in common in response to directional versus non-directional stimuli. These results suggest commonalities in the neurocognitive mechanisms underlying the automatic attentional shifts triggered by gaze, gestures, and symbols.

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Introduction

Sharing the direction of attentional focus represents an indispensable human ability that allows individuals to share critical information about the environment and to respond appropriately in coordination with others. Consistent with this notion, experimental psychological studies have revealed that the eye direction of another individual automatically triggers covert shifts in attention on the part of an observer (Frischen et al., 2007). Similarly, studies have revealed that automatic attentional shifts can be triggered by hand-pointing gestures (Langton and Bruce, 2000; Sato et al., submitted) and symbolic cues such as arrows (Hommel et al., 2001; Ristic et al., 2002; Tipples, 2002). These data suggest that gaze, gestures, and symbols automatically elicit coordinated attention.

Some previous neuroimaging studies have described the involvement of the posterior superior temporal sulcus (STS) in the processing of eye gaze (Puce et al., 1998; Wicker et al., 1998; Hoffman and Haxby, 2000; Hooker et al., 2003; Pelphrey et al., 2003; Sato et al., 2008). For example, the fMRI study of Hoffman and Haxby (2000) showed that directional eye gaze activated the left posterior STS and the bilateral intraparietal sulcus more than did non-directional eye gaze. The activated areas correspond to the STS region (Allison et al., 2000), which includes the posterior STS and the adjacent middle and

superior temporal gyri. Based on anatomical and functional evidence, the STS region has been proposed as homologous to the monkey anterior STS (Allison et al., 2000; Halgren et al., 1999; however, see Beauchamp, 2005), which contains neurons that respond strongly to the eyes (Perrett et al., 1985). A lesion study also showed that damage to the STS region impaired recognition of eye direction (Campbell et al., 1990). Human neuroimaging and lesion studies have indicated that the posterior parietal, including the intraparietal sulcus, is involved in attentional tasks (Corbetta, 1998). Based on this evidence, some authors (e.g., Hoffman and Haxby, 2000) have proposed that directional eye gaze is processed in the STS region and that attentional shift is automatically triggered by activity in the parietal regions.

Single-unit recording studies in monkeys, however, have indicated that the STS is not active in response to eyes specifically, but also respond to other social attention signals such as bodily gestures (Jellema and Perrett, 2005); cells in the STS, which are active in response to certain eye directions, are also active in response to the same directional movements of the head and body. Similarly, neuroimaging studies in humans have indicated that the observation of bodily gestures activates the STS region, which is also active in response to eyes (Allison et al., 2000). For example, some neuroimaging studies have reported that the STS region was active while viewing hand movements (Bonda et al., 1996; Pelphrey et al., 2004; Wheaton et al., 2004; Thompson et al., 2007) and hand gestures (Grezes et al., 1999; Nakamura et al., 2004). Thus, it is possible that the pointing gestures may be processed by the same neuronal mechanism in the STS region as those for the eyes.

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Furthermore, a meta-analysis of neuroimaging data has shown shared cortical regions involved in attentional shifts and gaze perception (Grosbras et al., 2005); the STS region, which is activated in response to eyes, is activated by peripheral sensory stimuli, which induce an automatic attentional shift. In addition to the STS region, the inferior parietal lobule and inferior frontal gyrus in the right hemisphere are commonly activated in visually-triggered attentional shifts and gaze perception. These data suggest that the fronto-parietal and temporal brain network could be commonly related to processing attention-triggering stimuli.

Based on these data, we hypothesized that these brain regions are commonly involved in the automatic attentional shifts triggered by gaze, gestures, and symbols. To evaluate this hypothesis, we used fMRI to examine brain activity while participants passively observed directional/non-directional stimuli, including eyes, hands, and arrows. We performed cognitive conjunction analyses (Price and Friston, 1997; Friston et al., 1999, 2005) to depict the commonalities in the brain activity for directional versus non-directional conditions across stimulus types. We also examined the differences in brain activity by analyzing the interactions between stimulus type and directional condition.

Material and methods

Participants

Fifteen healthy volunteers (11 women and 4 men; mean age, 22.4 years) participated in this experiment. All participants were right-handed and had normal or corrected-to-normal visual acuity. All participants gave informed consent to participate in the study, which was conducted in accord with institutional ethical provisions and the Declaration of Helsinki. Although two additional participants actually participated, their data were not analyzed because they displayed obvious drowsiness.

Experimental design

The experiment was constructed as a within-subject two-factorial design, with stimulus type (eyes/hand/arrow) and directional condition (directional/non-directional) as the factors. To implement a

simple experimental design appropriate for cognitive conjunction analyses and to diminish contamination by motor-related components to the brain activity, participants passively viewed the stimuli under a dummy target detection task.

Stimuli

The directional stimuli were represented by eyes, hands, or arrows (Fig. 1). For eye stimuli, we prepared gray-scale photographs of full-face, neutral expressions displayed by four females and three males looking left. For hand stimuli, we prepared gray-scale photographs of hands pointing to the left. The arrow stimuli pointing left consisted of horizontal lines subtending 2.0–4.0° horizontally and two oblique lines, which tilted 30–60° from the horizontal line. Mirror images of these stimuli were created using Photoshop 6.0 (Adobe) and used as the stimuli indicating direction to the right.

Stimuli that were neutral for direction were also prepared. For eye stimuli, gray-scale photographs of full-face neutral faces gazing straight ahead were prepared. For hand stimuli, gray-scale photographs of fists were prepared. For arrow stimuli, a lozenge was constructed using the same horizontal and oblique lines used for the directional stimuli. The mirror images of these stimuli were also created to produce the same number of stimuli as presented in the directional condition.

All stimuli were depicted in a rectangle on a gray plane background, subtending 6.3° vertical × 5.0° horizontal. The mean luminance of all images was made constant using MATLAB 6.0 (Mathworks).

In order to ensure that the directional stimuli could trigger automatic attentional shifts, we conducted a preliminary behavioral experiment using a cuing paradigm with 15 participants (11 women and 4 men; mean age, 19.1 years), none of whom took part in the subsequent fMRI experiment. The experiment was conducted on an individual basis outside the scanner. The stimuli were presented on a 19-inch CRT monitor (UltraScan P991, Dell). The experiment consisted of a total of 252 trials. Trials were presented in random order. In each trial, after a central fixation cross appeared for 500 ms, a directional or non-directional stimulus was presented at the center of the screen for 300 ms. Then, a target (a small open circle) was presented in either the left or the right visual field until a response

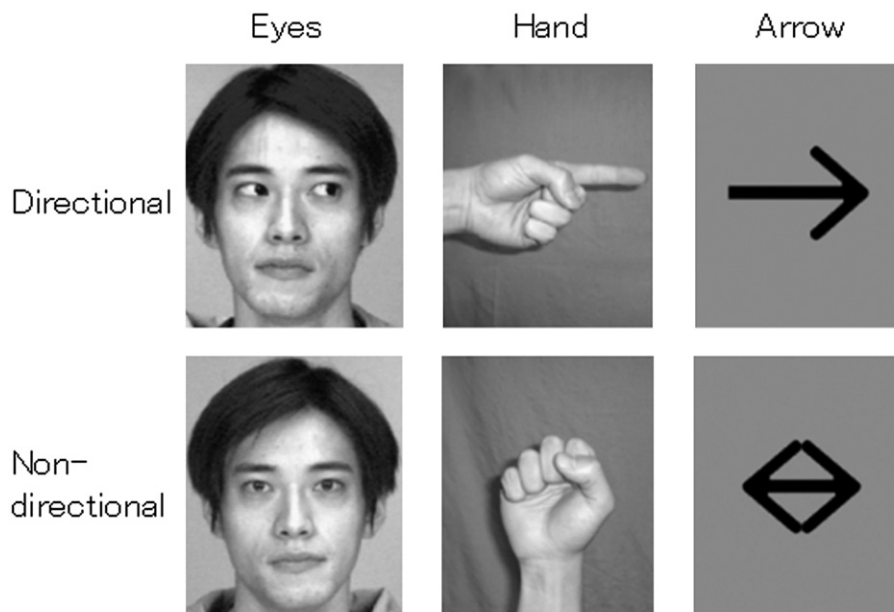


Fig. 1. Examples of stimuli.

was elicited. The participants were asked to localize the target by pressing a button as quickly as possible. Participants were told that the stimuli preceding the targets were not predictive. A 3 (stimulus type: eyes/hand/arrow) × 3 (cue–target validity: valid/neutral/invalid) repeated-measures analysis of variance (ANOVA) was conducted for the correct reaction times (RTs; Fig. 2). The results revealed a significant main effect of cue–target validity ($F(2,28)=43.25, p<.001$). There were no other significant main effects or interactions ($ps>.1$). Tukey's multiple comparisons for the main effect of cue–target validity indicated that the RTs for the valid conditions were shorter than those for either the neutral or invalid conditions, and that the RTs for the neutral condition were shorter than those for the invalid condition ($ts(14)>4.43; ps<.001$). As confirmation, the simple main effects of cue–target validity were analyzed, and results showed the same patterns for all stimulus types ($ts(14)>3.44; ps<.005$). These results are consistent with those of previous behavioral studies (e.g., Hietanen, 1999; Hommel et al., 2001; Sato et al., submitted) and indicated that the directional eyes, hands, and arrows used in the present fMRI study were consistently able to trigger automatic attentional shifts.

Presentation apparatus

The events were controlled using SuperLab Pro 2.0 (Cedrus) implemented on a Windows computer (Dimension 8000, Dell). The stimuli were projected from a liquid crystal projector (DLA-G11, Victor Company) to a mirror that was positioned in a scanner in front of the participant.

Procedure

Each participant participated in three experimental sessions. Each session lasted 8 min and consisted of eight 30 s on-epochs, during which experimental stimuli were presented, interleaved with eight 30 s off-epochs, during which a fixation point was presented in the center of the screen. Each session was conducted for one of the three stimulus types (i.e., eyes, hand, or arrow). The order of stimulus type was counterbalanced across participants. Each of the two directional conditions (directional, non-directional) was presented in each epoch within each session. The order of epochs within each session was counterbalanced across participants.

In each epoch, 30 trials (each lasting 1000 ms) were conducted. In each trial, after the central presentation of a black cross as a fixation point lasting 500 ms, the stimulus was presented for 500 ms in the

center of the screen. In two trials in each epoch, a red cross was presented instead of the stimulus. The order of trials within each epoch was pseudo-randomized.

The participants were instructed to fixate on the center of the screen (i.e., where the fixation point was presented during rest periods). They were instructed to detect a red cross, and then to press a button as quickly as possible. This dummy task was prepared to maintain the arousal and attention of the participants. Participants responded using the index finger of their right hand.

To confirm that the brain activations were not explained by eye movement artifacts, we tested five of the participants while monitoring eye movements in the scanner after image acquisition. The procedure was identical to that of the experiment. Horizontal eye movements were monitored using MR-Eyetracker (Cambridge Research Systems). The number of horizontal eye movements exceeding 5° was minimal under all conditions ($n<1$ during each epoch) and did not differ significantly across stimulus types or direction conditions (two-way repeated-measures ANOVA, $p>.1$).

Image acquisition

Image scanning was performed on a 1.5 T scanning system (MAGNEX ECLIPSE 1.5 T Power Drive 250, Shimadzu Marconi, Kyoto, Japan) using a standard radio frequency head coil for signal transmission and reception. A forehead pad was used to stabilize the head. The functional images consisted of 26 consecutive slices parallel to the anterior–posterior commissure plane, covering the whole brain except for the cerebellum. The $T2^*$ weighted gradient echo-planar imaging sequence was used with the following parameters: TR/TE=3000/60 ms; FA=90°; matrix size=64×64; and voxel size=3×3×3 mm. Before the acquisition of functional images, a $T2$ weighted anatomical image was obtained in the same plane as the functional images using a fast spin echo sequence (TR/TE=9478/80 ms, FA=90°; matrix size=256×256; voxel size=0.75×0.75×3 mm; number of echoes=16). An additional high-resolution anatomical image was also obtained using a 3D RF-FAST sequence (TR/TE=12/4.5 ms; FA=20°; matrix size=256×256; voxel dimension=1×1×1 mm).

Image analysis

Image and statistical analyses were performed using the statistical parametric mapping package SPM2 (<http://www.fil.ion.ucl.ac.uk/spm/>) implemented in MATLAB 6.5 (Mathworks). First, we conducted a slice-timing correction to correct for differences in slice acquisition times during echo-planar scanning in ascending order. We interpolated and resampled the data so that each time series had been obtained at slices that would be acquired at the same time as the reference slice. The reference slice was the middle one. The images were then realigned using the first image as a reference. Data from all participants showed small motion correction (<1 mm). The $T2$ weighted anatomical images that were scanned in planes identical to the functional imaging slices were coregistered to the first scan in the functional images. The coregistered $T2$ weighted anatomical images were then normalized to a standard $T2$ template image, as defined by the Montreal Neurological Institute (MNI), which involved linear and non-linear three-dimensional transformations (Friston et al., 1995; Ashburner and Friston, 1999). The parameters estimated from this normalization process were then applied to each of the functional images. Finally, these spatially normalized functional images were resampled to a voxel size of $2\times 2\times 2$ and smoothed with an isotropic Gaussian kernel (10 mm) to compensate for anatomical variability among participants. The high-resolution anatomical images were also normalized using the same procedure.

We searched for significantly activated voxels using random-effects analysis. First, we performed single-subject analyses (Friston

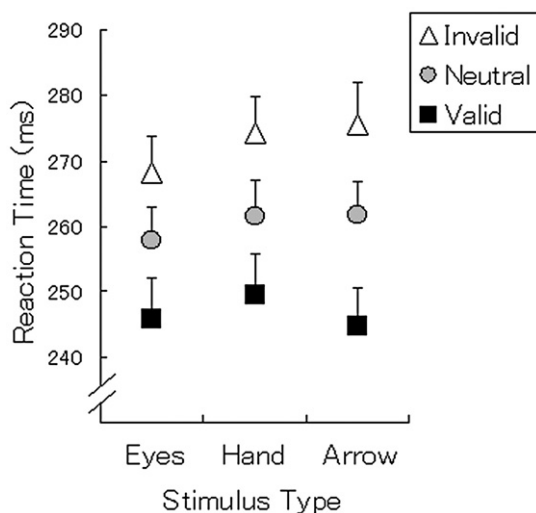


Fig. 2. Mean (with SE) reaction times in the preliminary behavioral experiment.

et al., 1994; Worsley and Friston, 1995). In the single-subject analyses, the design matrix contained six task-related regressors (directional eyes, non-directional eyes, directional hand, non-directional hand, directional arrow, and non-directional arrow), which were modeled by convolving a boxcar function at each condition with a canonical hemodynamic response function (HRF). We used the high-pass filter, composed of the discrete cosine basis function with a cut-off period of 128, to eliminate an artifactually low frequency trend. Serial autocorrelation, assuming a first-order autoregressive model, was estimated from the pooled active voxels using a restricted maximum likelihood (ReML) procedure and used to whiten the data and design matrix (Friston et al., 2002). The least-square estimation was performed on the high-pass-filtered and pre-whitened data and design matrix, giving the estimated parameters. The weighted sum of the parameter estimates in the single-subject analysis constituted contrast images that were used for the second level analysis. A random-effects model analysis was conducted to make statistical inferences at the population level (Holmes and Friston, 1998).

Initially, the contrast between directional and non-directional conditions was tested for each stimulus type. Voxels were identified as significantly activated if they reached the height threshold of $p < .01$ (uncorrected), with the extent threshold of 30 voxels. These analyses were conducted as exploratory analyses for the following statistical tests of commonalities and differences.

Next, to test our prediction that common activity would emerge in response to directional versus non-directional conditions across stimulus types, two types of cognitive conjunction analyses were conducted. We focused on the brain regions that were significantly activated in both analyses.

First, we performed a traditional analysis using interaction masking (Price and Friston, 1997). For this analysis, we conducted a main effect analysis of directional condition (directional versus non-directional) using the T -statistic. To search for brain areas that showed similar activity across stimulus types (eyes, hand, and arrow),

the main effect was exclusively masked by the F -tests of interactions. For details, voxels where there were significant interactions between effects at a threshold of $p < .1$ (uncorrected) were eliminated from the statistical parametric map of the main effect. For the main effect contrast, voxels were identified as significantly activated if they reached the height threshold of $p < .01$ (uncorrected), with the extent threshold corrected for multiple comparisons ($p < .05$). For the brain regions identified in a previous meta-analysis as commonly activated in response to attention and gaze perception tasks (the STS region, the inferior parietal lobule, and the inferior frontal gyrus; Grosbras et al., 2005), we used small-volume correction (SVC) using 10 mm radius spheres. Other areas were corrected for the entire brain volume.

Second, to further confirm the common activity detected by the aforementioned interaction masking analysis, we conducted a newly developed conjunction analysis with the global null hypothesis (Friston et al., 1999, 2005). In this analysis, we used the minimum T -statistic over three orthogonal contrasts, each of which was a main effect of directional condition (directional versus non-directional) for different stimulus type (eyes, hand, and arrow). An intermediate null hypothesis was used to infer a conjunction of $k > 1$ effects at significant voxels (Friston et al., 2005). Voxels were identified as significantly activated if they reached the height threshold of $p < .01$ (uncorrected) with the extent threshold of 30 voxels.

Finally, to test the differences in the brain activity under directional versus non-directional conditions across stimulus types, interactions between stimulus type and directional condition were analyzed. We analyzed the specific instances in which higher activity showed greater association with one stimulus type than with the other two stimulus types. For example, the interaction involving higher activity specifically for directional eyes was tested as follows: $\{(directional\ eyes - non-directional\ eyes) - 1/2 \times [(directional\ hand - non-directional\ hand) + (directional\ arrow - non-directional\ arrow)]\}$. Voxels were identified as significantly activated if they reached the height

Table 1

Brain regions that exhibited significant activation in response to directional versus non-directional conditions for each stimulus type

Brain region	BA	Eyes				Hand				Arrow			
		Coordinates			Z-value	Coordinates			Z-value	Coordinates			Z-value
		x	y	z		x	Y	z		x	y	z	
R. inferior occipital gyrus	18	42	-78	-12	3.83					38	-84	-10	3.31
R. middle occipital gyrus	18												
R. lingual gyrus	18					14	-78	-16	2.78				
R. fusiform gyrus	19	40	-50	-20	4.61					42	-66	-20	3.19
R. angular gyrus	39					32	-58	34	3.18				
R. inferior parietal lobule	40	34	-36	30	2.77	48	-52	52	3.04	44	-52	48	3.05
R. superior parietal lobule	7					38	-62	52	3.55	38	-58	58	3.46
R. inferior temporal gyrus	37									40	-60	2	4.59
R. middle temporal gyrus	37									52	-66	2	4.55
R. superior temporal gyrus	22	48	-44	10	2.59					60	-42	20	3.73
R. amygdala	-	20	-6	-6	2.57								
R. thalamus	-					12	-14	-2	3.19				
R. cingulate gyrus	24	12	0	26	2.83					12	0	28	3.35
R. caudate nucleus (tail)	-									16	-24	22	3.07
R. caudate nucleus (body)	-	18	6	24	2.62					10	16	18	2.81
R. precentral gyrus	6									42	4	40	2.87
R. inferior frontal gyrus	44	52	20	32	2.58	44	20	36	2.60	28	4	28	3.25
R. inferior frontal gyrus	45	54	30	18	2.63								
R. middle frontal gyrus	6									40	4	52	3.19
L. inferior occipital gyrus	18	-14	-94	-10	3.00					-36	-88	-4	3.41
L. middle occipital gyrus	18									-26	-88	10	2.78
L. lingual gyrus	18					-16	-84	-20	2.60				
L. fusiform gyrus	19	-40	-56	-22	3.48					-42	-60	-14	3.36
L. inferior parietal lobule	40									-40	-40	42	2.85
L. middle temporal gyrus	37									-40	-56	10	3.17
L. superior parietal lobule	7									-34	-48	60	3.08
L. precentral gyrus	6									-32	-14	62	2.89

The coordinates of activation foci in the MNI system are shown. BA: Brodmann areas.

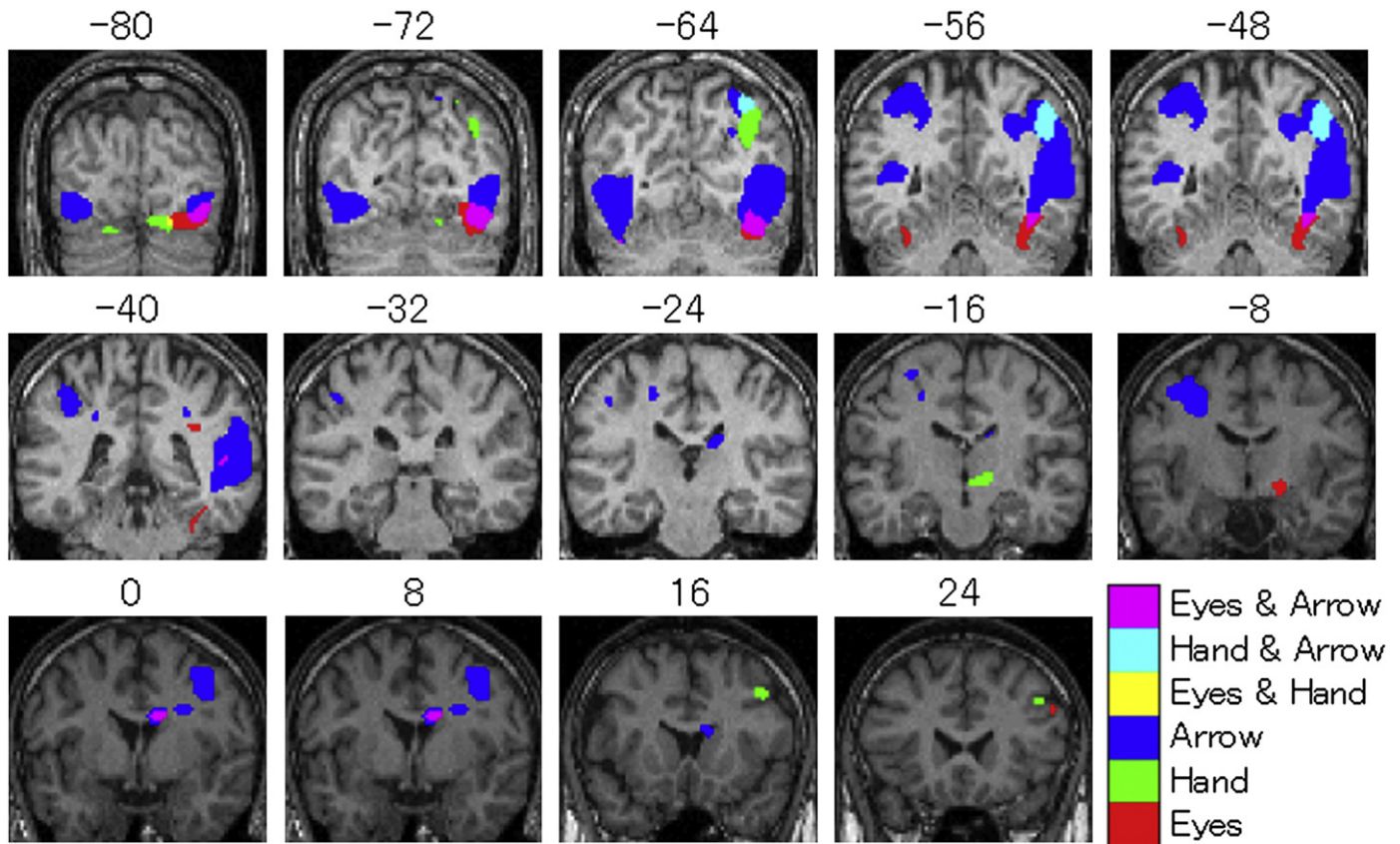


Fig. 3. Statistical parametric maps indicating the brain regions that were activated in response to directional versus non-directional conditions for eyes, hand, and arrow conditions. The area is overlaid on the normalized anatomical MRI of one of the participants in this study. The numbers above the slices indicate y-axis MNI coordinates.

threshold of $p < .01$ (uncorrected) with the extent threshold corrected for multiple comparisons ($p < .05$).

Results

Behavioral performance

Performance on the dummy target detection task was close to perfect (correct identification rate of 97.9%). There were no significant differences among stimulus types or directional conditions in the numbers of correct responses or RTs (two-way repeated-measures ANOVA, $p > .1$).

Neural activity for each stimulus type

The contrast between directional and non-directional conditions was tested for each stimulus type (Table 1; Fig. 3). In all three stimulus type conditions, significant activity was detected in the right inferior parietal lobule, the right ventral premotor region, and the bilateral posterior visual cortices. Activity of the right STS region was found for eyes and arrows; this was also the case for hands when a more liberal height threshold was used ($p < .05$, uncorrected). Significant activity in response to arrows in particular was found in some brain regions, including the right middle and inferior temporal gyri and the left superior parietal lobule.

Table 2
Brain regions that exhibited significant activation in response to directional versus non-directional conditions for the main effect analysis with interaction masking (left) and the conjunction analysis with the global null hypothesis (right)

Brain region	BA	Common activation in both analyses	Interaction masking				Conjunction with global null hypothesis			
			Coordinates			Z-value	Coordinates			Z-value
			x	y	z		x	y	z	
R. inferior occipital gyrus	18	*	38	-84	-10	4.23	36	-86	-8	4.37
R. middle occipital gyrus	18	*	20	-92	8	2.75	22	-92	6	3.19
R. fusiform gyrus	19	*	36	-64	-20	4.01	32	-64	-20	3.63
R. supramarginal gyrus	40	*	64	-46	20	3.22	62	-50	28	3.72
R. inferior parietal lobule	40	*	46	-50	48	3.47	42	-48	46	3.67
R. superior parietal lobule	7	*	38	-62	54	4.06	32	-62	54	4.24
R. middle temporal gyrus	21	*	52	-38	-4	2.51	52	-36	-6	3.17
R. superior temporal gyrus	22	*	64	-44	12	3.24	64	-46	16	3.19
R. inferior frontal gyrus	45	*	48	26	22	2.89	48	24	20	3.57
R. middle frontal gyrus	8						44	10	48	3.83
R. middle frontal gyrus	46						40	36	34	3.03
L. inferior occipital gyrus	18						-20	-90	-4	3.88
L. fusiform gyrus	19						-32	-74	-10	3.75

The coordinates of activation foci in the MNI system are shown. BA: Brodmann areas.

Commonalities in neural activity

In both the interaction masking (Price and Friston, 1997) and the conjunction analysis with the global null hypothesis (Friston et al., 1999, 2005), the contrast between directional and non-directional conditions revealed significant activation in broad ranges of the STS region and in the inferior parietal lobule in the right hemisphere (Table 2, Fig. 4). The right ventral premotor region, including the pars opercularis of the inferior frontal gyrus, was also significantly activated. In addition, significant activation of the occipital cortices was observed in the right hemisphere.

Differences in neural activity

No specific activity indicated significant activation in response to directional versus non-directional eyes. However, it is interesting to note that there was a small activation in the right amygdala in response to directional versus non-directional eyes ($x=-22, y=-8, z=-14; Z=2.40$). No specific activity indicated significant activation in

response to hand stimuli. Significant activation was observed in the right posterior temporal cortices, including the activation foci of the inferior and middle temporal gyri, and the left superior parietal lobule, extending into the precentral gyrus, in response to directional versus non-directional arrows (Table 3).

Discussion

Commonalities

The STS region, the inferior parietal lobule, the inferior frontal gyrus, and the occipital cortices in the right hemisphere showed higher activity in response to directional than to non-directional eye, hand, and arrow stimuli. The activation of the STS region and posterior parietal cortices in response to directional versus non-directional eyes is consistent with the results of previous studies that compared directional versus non-directional eyes (e.g., Hoffman and Haxby, 2000). Our results extend the notion that the same brain regions are active in the processing of directional stimuli depicting hands or

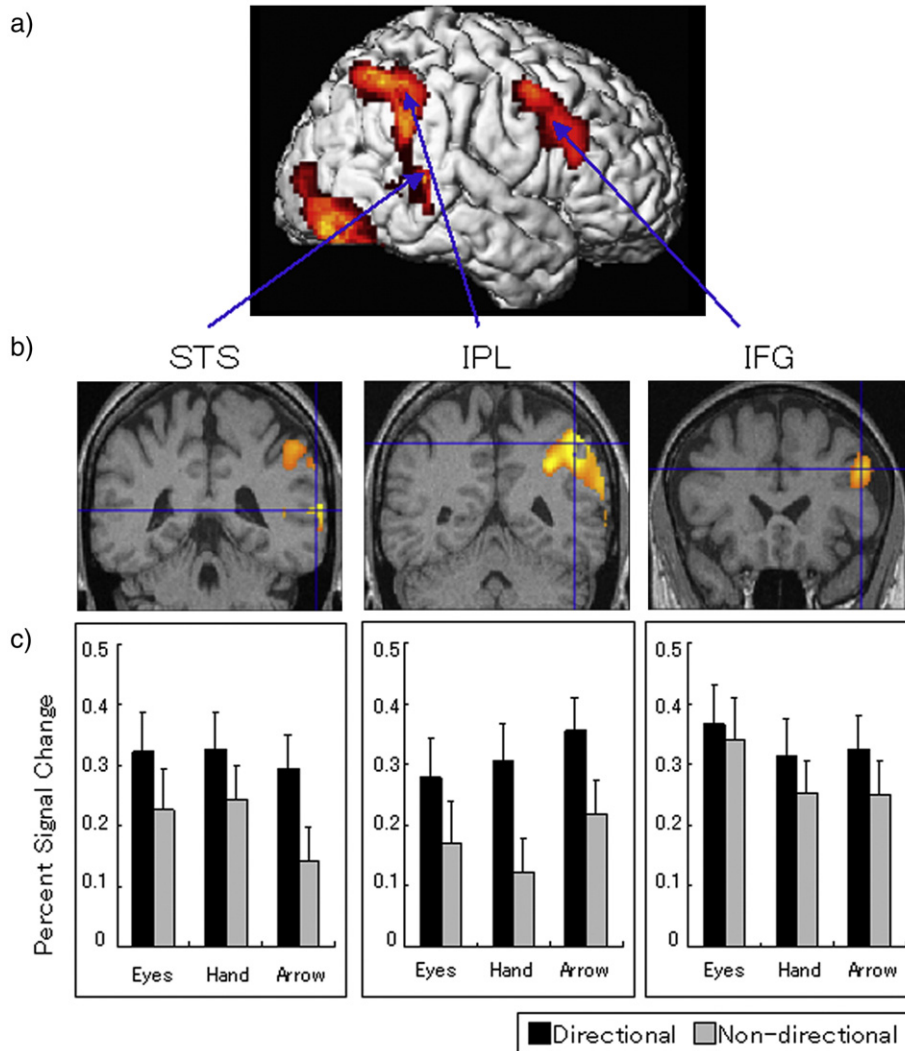


Fig. 4. (a) Statistical parametric maps indicating the brain regions that were activated in common in response to directional versus non-directional stimuli depicting eyes, hands, and arrows. The right hemisphere is shown. The areas of activation are rendered on spatially normalized brains. (b) Statistical parametric maps of the representative brain regions that exhibited higher activation for directional versus non-directional stimuli depicting eyes, hands, and arrows. The area is overlaid on the normalized anatomical MRI of one of the participants involved in this study. STS=superior temporal sulcus region; IPL=inferior parietal lobule; IFG=inferior frontal gyrus. (c) Mean percent signal changes (with SE) of representative brain regions that were highly activated in response to directional versus non-directional stimuli depicting eyes, hands, and arrows. The data were calculated by first sampling the spherical voxels of interest (10 mm radius) of these regions at the sites of peak activation in comparing directional versus non-directional conditions and then subtracting the mean signal value of the resting condition (baseline) obtained from those in the activation periods. Because of the time lag of hemodynamic responses, the first two images of each period were discarded.

Table 3
Brain regions that exhibited significant activation in response to directional versus non-directional conditions specifically for arrow stimuli

Brain region	BA	Coordinates			Z-value
		x	y	z	
R. inferior temporal gyrus	37	42	-60	4	4.47
R. middle temporal gyrus	37	52	-66	2	4.19
L. superior parietal lobule	7	-16	-52	46	3.22
L. superior parietal lobule	2	-28	-48	60	3.65
L. post central gyrus	2	-44	-26	44	3.28
L. precentral gyrus	6	-32	-8	42	3.14

The coordinates of activation foci in the MNI system are shown. BA: Brodmann areas.

arrows. The inferior frontal gyrus was also active while viewing these stimuli. These results are in accordance with a meta-analysis of neuroimaging data that indicated that these areas are commonly activated in visual attention and gaze perception (Grosbras et al., 2005). However, Grosbras et al. (2005) noted that the meta-analysis included methodologically different studies, particularly in regard to gaze, and that no single study had revealed such commonality. In the present study, we found that a shared neural network was active while viewing directional stimuli depicted by gaze, gestures, and symbols.

Some authors have proposed that the STS region is involved in the visual analysis of gaze direction. However, Allison et al. (2000) reviewed the neuroscientific data and proposed that the observation of bodily gestures also activates the STS region. For example, some neuroimaging studies have reported that the STS region was active while hand movements were viewed (e.g., Bonda et al., 1996). These data suggest that the STS region may be involved not only in gaze-related functions but also in more general functions related to biologically significant signals.

Furthermore, a lesion study in monkeys questioned whether the activity of the STS neurons was specifically related to biological stimuli (Eacott et al., 1993). In this study, the researchers damaged the monkeys' STS region and examined their ability to learn to visually discriminate character shapes and orientation and gaze direction. Monkeys with STS lesions demonstrated general impairment in visual discrimination that was not limited to gaze direction. In the context of our data showing the common activation of the STS region in response to gaze, hands, and arrows, these results suggest that the STS region is related to general functions, and not specifically to biological stimuli.

Experimental psychological studies indicate that eyes (Frischen et al., 2007), hands (e.g., Sato et al., submitted), and arrows (e.g., Hommel et al., 2001) commonly trigger automatic attentional shifts. Consistent with these behavioral findings, a meta-analysis of neuroimaging data found common activity in the STS region in regard to attentional shifts and gaze perception (Grosbras et al., 2005). Neuropsychological studies in humans have also shown that damage to this region impairs general stimulus-driven attention (Karnath, 2001). These data suggest that activation of the STS region in response to directional stimuli could be involved in automatic attentional orienting towards the cued direction, regardless of the kind of attention-triggering stimulus.

Furthermore, our data indicated that along with the STS region, the inferior parietal lobule and the inferior frontal gyrus in the right hemisphere were active while viewing directional versus non-directional stimuli depicting gaze, hands, and arrows. The activation of these regions has consistently been observed in previous neuroimaging studies of stimulus-driven attentional shifts (Corbetta and Shulman, 2002). On reviewing the neuroimaging data, Corbetta and Shulman (2002) proposed that sensory stimuli of potentially high behavioral significance could reorient attention and that the ventral fronto-parietal network may be related to the processing of such behaviorally significant stimuli. In this theoretical framework, our results may be interpreted as indicating that all gaze, bodily gestures, and symbols represent behaviorally significant stimuli that induce

automatic attentional shifts. Thus, they commonly activate the neural network related to automatic attention reorientation, which specifically includes the STS region, the inferior parietal lobule, and the inferior frontal gyrus in the right hemisphere.

Our results showed the activation of the right occipital cortices in response to directional and non-directional cues. The activation of the occipital cortices has been reported in some previous studies of stimulus-driven attentional shifts (e.g., Downar et al., 2000) and could be interpreted as reflecting enhanced visual processing (Corbetta, 1998).

Our results showed activity primarily in the right hemisphere in response to directional cues. This pattern is consistent with previous neuroimaging reports that have consistently indicated right hemispheric dominance in attentional tasks (e.g., Downar et al., 2000). A recent behavioral study also indicated that automatic attentional shifts triggered by eye gaze were dominant in the right hemisphere (Okada et al., 2006). It may be possible to interpret this right hemispheric dominance in the context of the more general literature addressing visual spatial processing. Some lesion studies have shown that the STS region (Karnath, 2001), the inferior parietal lobule (Mort et al., 2003), and the inferior frontal gyrus (Husain and Kannard, 1996) of the right hemisphere were involved in spatial awareness and exploration. These data suggest that the right hemispheric dominance in the present study may reflect the spatial processing triggered by directional gaze, gestures, and symbols.

Our results showed commonalities in brain activity while viewing attention-triggering stimuli depicted by gaze, gestures, and symbols. These results are consistent with those emerging from human developmental studies indicating that infants follow the direction of attention of adults, which were indicated by eyes or hand-pointing gestures (Csibra, 2003). Animal studies have also demonstrated that monkeys follow the direction of gaze of other individuals (Emery et al., 1997). Furthermore, an animal study has indicated that chimpanzees showed exogenous attentional shifting while viewing arrows (Itakura, 2001). These developmental and comparative data suggest that a shared neurocognitive mechanism underlying the automatic attentional shifts in response to gaze, gestures, and some kinds of symbols may have developed innately in human beings through the evolutionary process.

It should be noted that a previous study (Hietanen et al., 2006) has reported partially conflicting results regarding STS activity in response to eyes and arrows. That study reported that the STS region was active in response to directional versus non-directional arrows, but not directional versus non-directional eyes. This difference in results may be explained in terms of the methodological differences between studies. First, whereas Hietanen et al. (2006) used schematic drawings to depict eyes condition, we used photographic stimuli. Schematic drawings lack ecological validity compared to photos. A previous subdural electroencephalographic study has reported that the amplitudes of some face-related electrophysiological components in the STS region were smaller for line-drawings than for photographs of faces (McCarthy et al., 1999). Hence, our use of photographic stimuli might have enhanced the response of the STS region. Second, whereas Hietanen et al. (2006) conducted separate contrasts for each stimulus type and tested the overlap of clusters, we conducted statistical conjunction analyses. Our results pertaining to the contrasts for each stimulus type indicated that the activity of the STS region was more evident in response to arrows than to eyes, as Hietanen et al. (2006) found; however, our conjunction analyses detected activation of this region common to all stimulus types. We believe that conjunction analyses are more sensitive for analyzing commonalities in brain activity.

Differences

Some brain regions showed differential activity in response to directional versus non-directional conditions across stimulus types.

In particular, the right inferior and middle temporal gyri and the left superior parietal lobule showed activation only in response to directional arrows. The activity in the broad region of the temporal cortices, including the posterior middle temporal gyrus and the left superior parietal lobule, is consistent with data emerging from a previous study that investigated the observation of symbols associated with traffic rules (Donohue et al., 2005). This study further compared correct versus incorrect symbols and found that the posterior middle temporal gyrus was more active in response to correct than to incorrect symbols. Based on these results, the researchers suggested that the posterior middle temporal gyrus might play a role in the retrieval of the meanings of the symbols. In the context of these data, the brain regions identified by the current study may also be related to cognitive processing involved in the meanings implied by directional symbols.

We found a small activation in the amygdala specifically in response to directional eyes. This finding is consistent with evidence from recent lesion studies reporting that damage to the amygdala impaired automatic attentional shifting by eyes (Akiyama et al., 2007; Okada et al., 2008). A previous electrophysiological study in monkeys showed that some neurons in the amygdala were selectively activated for faces (Leonard et al., 1985). Together with these data, our results suggest that the amygdala may be specifically related to the processing of directional eyes.

Although our results did not show clear differences across stimulus types, this may be attributable to our task, in which only the directionality was manipulated and participants passively viewed the stimuli. Previous neuroimaging studies using gaze, gestural, or symbolic stimuli have suggested that specific activity can be connected to certain stimulus types. For example, Kampe et al. (2001) showed that attractiveness ratings for eyes were positively correlated with the activity of the ventral striatum. Lotze et al. (2006) reported that the observation of emotional gestures activated the ventrolateral prefrontal cortex. Donohue et al. (2005) showed that effortful retrieval of newly learned meanings for symbols activated the dorsolateral prefrontal cortex. It would be interesting in future studies to apply cognitive manipulations to further reveal commonalities and differences in regard to the processing of gaze, gestures, and symbols.

Methodological considerations

To analyze commonalities in brain activity, we conducted two types of conjunction analyses, the interaction masking (Price and Friston, 1997) and the conjunction analysis with the global null hypothesis (Friston et al., 1999, 2005), and focused on the brain regions producing significant results in both analyses. The interaction masking test was the first conjunction test in which the statistical map of main effect was exclusively masked by the significant interaction map regarded as positive for the conjunction. This analysis can detect the common activations across contrasts, discounting the effects not common to all contrasts (Price and Friston, 1997). To avoid potential errors in the use of interaction masking alone, we used this analysis along with conjunction analysis with the global null hypothesis. The latter analysis can reveal the brain regions where the contrasts are consistently high and jointly significant (Friston et al., 2005). We also verified the existence of common effects by plotting the signal changes within the regions detected by these statistical tests. We believe that our cautious procedure correctly evaluated the commonalities in brain activity.

An alternative approach to test the commonalities in brain activity may be a conjunction analysis with a conjunction null hypothesis (Nichols et al., 2005). However, this method has been criticized as too conservative and hence as causing false negative errors in neuroimaging data analysis, especially considering the problem of multiple comparisons (Friston et al., 2005). Our preliminary analyses consistently showed that the test of Nichols et al. (2005) produced

conservative results relative to the present two types of analyses; for example, we found activity of the right STS region only when we used a more liberal height threshold of uncorrected $p < .05$. Further methodological studies may be necessary to determine the definitive procedure for assessing commonalities in brain activity.

One methodological limitation of this study should be noted. Because we did not use a cueing paradigm during image scanning, the direct link between neural activity and behavioral performance remained untested. We used a simple two-factorial design without a target factor in the scanner because the cognitive conjunction analysis was not appropriate for implementation of complex factorial designs (cf. Friston et al., 2005). Future research that examines the relationship between brain activity and behavioral performance may provide further evidence regarding the brain mechanisms involved in the cognitive functions subserved by the brain activity we observed.

Conclusion

Our results showed that the STS region, the inferior parietal lobule, the inferior frontal gyrus, and the occipital cortices in the right hemisphere were, together, more active in response to directional than non-directional stimuli, including eyes, hands, and arrows. These results suggest commonalities in the neurocognitive mechanisms underlying the automatic attentional shifts triggered by gaze, gestures, and symbols.

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