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Title:

Commonalities and differences in the spatiotemporal neural dynamics associated with automatic attentional shifts induced by gaze and arrows

Running title:

Neural activation to gaze and arrows

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Abstract

Gaze and arrows automatically trigger attentional shifts. Neuroimaging studies have identified a commonality in the spatial distribution of the neural activation involved in such attentional shifts. However, it remains unknown whether these activations occur with common temporal profiles. To investigate this issue, magnetoencephalography (MEG) was used to evaluate neural activation involved in attentional shifts induced by gaze and arrows. MEG source reconstruction analyses revealed that the superior temporal sulcus and the inferior frontal gyrus were commonly activated after 200 ms, in response to directional versus non-directional cues. Regression analyses further revealed that the magnitude of brain activity in these areas and in the bilateral occipital cortex was positively related to the effect of attentional shift on reaction times under both the gaze and the arrow conditions. The results also revealed that some brain regions were activated specifically in response to directional versus non-directional gaze or arrow cues at the 350–400-ms time window. These results suggest that the neural mechanisms underlying attentional shifts induced by gaze and arrows share commonalities in their spatial distributions and temporal profiles, with some spatial differences at later time stages.

Keywords: Attention orienting; Arrow; Gaze; Magnetoencephalography (MEG)

1 Introduction

Sharing attention with others allows individuals to share critical information regarding the environment and to respond appropriately in coordination with others. Gaze direction provides information about the direction of others' attention (Emery, 2000), and behavioral studies have shown that the eye gaze of others triggers attentional shifts (Frischen et al., 2007). For example, Friesen and Kingstone (1998) presented gaze cues at the center of a screen. Subsequently, a target appeared to the left or the right of the cue. Participants were asked to detect, localize, and identify the subsequent target. The results revealed that participants showed a shorter reaction time (RT) to gaze-at-targets (i.e., valid condition) than to non-gaze-at-targets (i.e., invalid condition). Attentional shifts occurred even when the cues were counterpredictive of the target locations (Driver et al., 1999) or were presented without the conscious awareness of the participant (Sato et al., 2007). These data indicate that gaze automatically triggers attentional shifts.

Symbols, such as arrows, are also important cues that signal attentional direction. Pioneering studies have demonstrated that arrows trigger attentional shifts only when participants intend to follow the direction of the cues (e.g., Posner, 1980). In line with this, some behavioral studies have demonstrated that, unlike gaze cues, arrow cues did not induce reflexive attention orienting in some situations; arrow cues did not trigger attention orienting when they were counterpredictive of a target location (Friesen et al., 2004) or had different characteristics (e.g., color) than that of the target (Ristic et al., 2007). Further, a recent study found a right-lateralized hemispheric asymmetry for attention orienting by gaze but not by arrow cues (Greene and Zaidel, 2011), suggesting that different psychological mechanisms were involved in the two types of cueing. However, other studies have shown that arrow cues automatically trigger attentional shifts in the same manner as do gaze cues (Hommel et al., 2001 and Tipples, 2002). Several recent studies have compared the behavioral effects of gaze and arrow cues using the cueing paradigm (Sato et al., 2010; Stevens et al., 2008 and Tipples, 2008). These studies found that both types of cues trigger attentional shifts even when they are counterpredictive of target locations (Tipples, 2008), induce enhanced response speed but not enhanced accuracy when discriminating the target following the cue (Stevens et al., 2008), and have comparable sensitivity to the stimulus onset asynchrony between cues and targets (Sato et al., 2010). These data suggest some common features in the psychological mechanisms underpinning the automatic attentional shifts triggered by gaze and arrows.

Recent functional magnetic resonance imaging (fMRI) studies have investigated the neural activity underlying the attentional shifts induced by gaze and arrow cues. Hietanen et al. (2006) demonstrated activation of the middle/inferior occipital area by gaze cues, whereas arrow cues induced activity in these regions as well as in areas in the fronto-parietal cortex. However, other fMRI studies have revealed common patterns of neural activation underlying the attentional shifts induced by gaze and arrows (Tipper et al., 2008 and Sato et al., 2009). Tipper et al. (2008) presented an ambiguous cue stimulus in the cueing paradigm and asked participants to view the cue stimulus as either an eye or an arrow. This study found that the distributed frontoparietal and posterior regions, which include the inferior frontal gyrus (IFG), posterior superior temporal sulcus (STS), inferior parietal lobule (IPL), and inferior occipital gyrus (IOG), were commonly activated during attentional shifts following gaze and arrow cues. Sato et al. (2009) investigated neural activation while participants passively observed the directional and non-directional cues of gaze and arrows. Brain regions, including the IOG, STS, IPL, and IFG in the right hemisphere, were commonly activated in response to directional versus non-directional gaze and arrow cues. In a study comparing gaze cues and different non-gaze cues (i.e., peripheral squares), Greene et al. (2009) also demonstrated that these two types of cues activated largely overlapping brain regions covering the aforementioned areas. Although these studies also found differences in neural activity in response to gaze and arrow cues (Sato et al., 2009 and Tipper et al., 2008), brain regions which showed distinct activations to gaze and arrow cues were not consistent across studies. These findings suggest that attentional shifts induced by gaze and arrow cues are implemented by the activation of common as well as different neural mechanisms.

However, due to the limited temporal resolution of the fMRI technology, questions about whether the neural activation in response to gaze and arrow cues occurs with common temporal profiles have remained unanswered. Commonalities in the spatial distribution of neural activations do not necessarily indicate a commonality of temporal profiles. Electrophysiological recordings, including electroencephalography (EEG) and magnetoencephalography (MEG), are appropriate tools to measure brain activity with high temporal resolution. A few previous EEG studies have investigated the processing of gaze and arrow cues (Brignani et al., 2009 and Hietanen et al., 2008). Brignani et al. (2009) evaluated neural responses in the cueing paradigm using directional gaze and arrows. Consistent with the results of the fMRI studies (Sato et al., 2009 and Tipper et al., 2008), similar spatial and temporal patterns of EEG activation were found in the posterior and frontal regions in response to directional cues. Hietanen et al. (2008) presented directional and non-directional gaze and arrow cues and found that some components in temporoparietal sites, specifically after 200 ms, were commonly activated in response to directional versus non-directional cues. A recent MEG study also compared the brain responses to gaze cues and to non-gaze cues (i.e., peripheral squares) and found very similar patterns in the time course of global field power (Nagata et al., 2012). In summary, these data suggest a certain level of commonality in the temporal profiles of brain activation in response to gaze and arrow cues. However, because of limitations in the spatial resolution of electrophysiological measures (Dale and Halgren, 2001), it remains unclear whether the activation of the specific brain regions identified in fMRI studies (Sato et al., 2009 and Tipper et al., 2008) exhibited common temporal profiles in response to gaze and to arrows.

In this study, we recorded MEG signals and conducted source-reconstruction analysis using fMRI data (Litvak et al., 2011) to investigate the temporal profiles of the neural activation involved in attentional shifts induced by gaze and arrows. Directional and non-directional gaze and arrow cues were presented, and participants were asked to localize the peripheral target as quickly and accurately as possible. Temporal profile analyses for the MEG signals in response to the directional and non-directional gaze and arrow cues were conducted in spatially restricted brain regions (i.e., the IOG, STS, IPL, and IFG) derived from a previous fMRI study (Sato et al., 2009). It was predicted that these brain regions would show a common temporal activation in response to directional versus non-directional cues. Regression analyses between brain activation and behavioral data were also conducted to test the prediction that the neural activation would be related to behavioral attentional shifts.

Additionally, we explored differences in the temporal pattern of activations in response to gaze and arrows. Based on previous behavioral (Friesen et al., 2004 and Ristic et al., 2007) and fMRI (Hietanen et al., 2006;

Tipper et al., 2008 and Sato et al., 2009) studies, it is plausible that the gaze and arrow cues could activate distinct in addition to common neural mechanisms. We explored the different spatiotemporal profiles of the MEG signals in response to gaze and arrow cues in the superior parietal lobule (SPL), the precentral gyrus (PCG), and the middle temporal gyrus (MTG), areas identified by a previous fMRI study (Sato et al., 2009).

2 Materials and methods

2.1 Participants

Eighteen volunteers participated in the study. All participants were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971), and had normal or corrected-to-normal visual acuity. All participants provided written informed consent prior to participation in this study, which was approved by the ethics committee of the Primate Research Institute, Kyoto University.

We analyzed the data from 13 volunteers (nine males; mean ± *SD* age 27.6 ± 5.8 years). Five volunteers (two females and three males) were excluded from the MEG analysis because the RT differences between invalid and valid conditions were not above zero, indicating no attentional shifts to the cued location under either gaze or arrow conditions. Our preliminary analyses confirmed that the same RT patterns were found even when these participants were included in the analyses.

2.2 Design

The experiment was constructed using a within-participant two-factorial design; cue type (gaze or arrow) and cue direction (directional or non-directional).

2.3 Stimuli

Gaze and arrow stimuli (Fig. 1) utilized by previous studies (Sato et al., 2009 and Sato et al., 2010) were employed here. These studies confirmed that these gaze and arrow cues trigger the same degree of attentional shift.

For directional gaze cues, we prepared gray-scale photographs consisting of full-face neutral expressions displayed by three females and three males looking left. Mirror images of these stimuli were created using Photoshop 6.0 (Adobe), and these were used as the stimuli indicating the right direction. For non-directional gaze cues, photographs of full-face neutral faces gazing straight ahead were also prepared.

For directional arrow cues, we created left-pointing stimuli consisting of horizontal lines subtending 4.0–8.0° horizontally with two oblique lines that tilted 30–60° from the horizontal line. Mirror images of these stimuli were created and used as right-pointing stimuli. Non-directional arrow cues were also prepared. Finally, a lozenge was constructed using the same horizontal and oblique lines that were used for the directional stimuli.

All stimuli were depicted within a rectangle, subtending 12.5° vertical × 10.0° horizontal, on a gray plane background. The mean luminance of all images was made constant using MATLAB 6.0 (Mathworks).

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Figure 1

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2.4 Apparatus

Events were controlled by Presentation software (version 10.0; Neurobehavioral System) implemented on a Windows computer. The stimuli were projected from a liquid crystal projector (DLA-G150CL; Victor) to a mirror that was positioned in front of the participants.

2.5 Procedures

In each trial, after a crosshair was presented at the center of the screen for 500 ms, a gaze or arrow cue (right, left, or non-directional) was presented at the same location for 500 ms. Then, the target letter “T” appeared to the left or the right side of the cue stimulus (Fig. 2). The presented cue did not predict the target location. Thus, the target appeared to each side of the cue stimulus 50% of the time. The participants were asked to specify as quickly and accurately as possible whether the target appeared on the left or the right side of the screen by pressing the corresponding button on the switch box using the right index or middle finger, respectively. The interval from target appearance to button response was measured. The target and cue remained on the screen until a response was made; if 1000 ms elapsed with no response, the target disappeared. After an 800–1200-ms inter-trial interval, the next trial started. The participants were told that the cues did not predict the target location and were instructed to fixate on the center of the screen.

The experiment consisted of gaze and arrow blocks, and block order was counterbalanced across participants. Each block included six blocks of 36 trials. Thus, a total of 432 trials (72 trials each for valid-gaze, invalid-gaze, non-directional-gaze, valid-arrow, invalid-arrow, and non-directional-arrow condition) were conducted. The trials were presented in random order, and participants were allowed to rest between blocks. Twenty practice trials preceded the experimental trials.

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Figure 2

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2.6 MEG acquisition

MEG acquisition was performed in an electromagnetically shielded room using a 210-channel whole-head supine-position system (PQ1400RM; Yokogawa). A forehead strap was used to stabilize head position. MEG data were sampled at 1000 Hz through a band-pass of 0.05–200 Hz. Vertical and horizontal electrooculograms (EOGs) were simultaneously recorded.

To measure head position within the MEG sensor system, five calibration coils were mounted on the participants' heads. An electromagnetic calibration of the coil positions was performed before each

MEG recording session. Participants' head shape and calibration coil positions were digitized with a three-dimensional (3D) laser-optical scanner and a stylus marker (FastSCAN Cobra; Polhemus) and were later used to co-register the MEG sensor locations to an anatomical space defined by an individual MRI.

2.7 Anatomical MRI acquisition

Anatomical MRI acquisition was performed on a 3 T scanning system (MAGNETOM Trio A, Tim System; Siemens) using a 12-channel head coil with a forehead pad used to stabilize head position. A T1-weighted high-resolution anatomical image was obtained using a magnetization-prepared rapid-acquisition gradient-echo (MP-RAGE) sequence (TR = 2250 ms; TE = 3.06 ms; IT = 900 ms; flip angle = 9°; field of view = 256 × 256 mm; voxel size = 1 mm × 1 mm × 1 mm).

2.8 Data analysis: behavioral performance

Data were analyzed using SPSS 10.0J (SPSS; Japan). As in previous studies (e.g., Langtone and Bruce, 1999), the median RT of correct responses was calculated for each condition and analyzed using a 2 (cue type) × 3 (cue-target validity) repeated-measures analysis of variance (ANOVA). In cases in which the assumption of sphericity was not met ($p < 0.05$, Mauchley's sphericity test), the Greenhouse–Geisser adjusted degree of freedom was used. Multiple comparisons were performed using Ryan's method. To confirm the results in the absence of parametric assumptions, we also performed Wilcoxon signed-rank tests. The results of all tests were considered statistically significant at $p < .05$.

2.9 Data analysis: MEG preprocessing and source reconstruction

2.9.1 Commonality.

Data analysis was conducted using Statistical Parametric Mapping software (SPM8 r4290; http://www.fil.ion.ucl.ac.uk/spm/). Continuous MEG data were epoched into 500-ms segments for each trial and down-sampled to 200 Hz; pre-stimulus baseline data were collected for 50 ms, and experimental data were collected for 450 ms after cue stimulus onset. The data were initially subjected to independent component analyses (ICA) for the purpose of artifact rejection using EEGLAB toolbox (http://sccn.ucsd.edu/eeglab/index.html). The ICA components (ICs) were visually inspected, and those representing eye artifact, heartbeat, or muscle activities were rejected. The rest of the ICs were projected back to the MEG sensor space to obtain a “clean” MEG signal. Threshold-based artifact rejection was also conducted. Any epochs containing a gradiometer amplitude ≥3000 fT/cm and an absolute EOG amplitude ≥80 μV were rejected as artifacts. The number of artifact-contaminated trials did not differ across conditions (mean ± $SD = 8.56 \pm 4.66$; $p > 0.1$, within-participant ANOVA). The pre-processed data were then low-pass filtered at 48 Hz, baseline corrected on the basis of the 50-ms pre-stimulus period, and averaged over trials by conditions for the following analyses.

For fMRI-constrained MEG source reconstruction, the restricted solution approach implemented in SPM8 (Litvak et al., 2011) was used, where a “hard” spatial prior derived from fMRI studies was imposed to solve the MEG inverse problem with a reduced source space. First, the cortical mesh on which the current dipoles were placed was created. The individual anatomical MRI of each participant was segmented and spatially normalized to the Montreal Neurological Institute (MNI) space. The inverse of this normalization transformation was then used to warp a canonical cortical mesh in the MNI space to the individual cortical mesh (Mattout et al., 2007). The cortical mesh described the source locations with 20,484 vertices (i.e., “fine” size). Next, the MEG sensors were co-registered to anatomical MRI data by matching the positions of three fiducials (nasion and R- and L-preauricular points) and head shape. The forward model could then be computed using a “single sphere” model by assuming that the orientations of the sources were normal to the cortical mesh.

The forward model was inverted using a parametric empirical Bayesian framework (Mattout et al., 2007) with the optimization of Multiple Sparse Priors (MSP) by a greedy search algorithm (Friston et al., 2008). To investigate the commonality of the brain activities induced by gaze and arrows, the inverse reconstruction used to compute cortical source activities was restricted to eight predefined regions of interest (ROIs; i.e., restricted solution approach). Based on a previous fMRI study (Sato et al., 2009), the brain regions that were more activated in response to directional versus non-directional gaze and arrow cues were selected. The center coordinates for the IOG, STS, IPL, and IFG in the right hemisphere were selected. A sphere with a 24-mm radius centered on the coordinates of each area was created. Although the original study (Sato et al., 2009) reported activation in only the right hemisphere, the hemispheric functional asymmetry in fMRI (Tipper et al., 2008), EEG (Brignani et al., 2009 and Hietanen et al., 2008) and behavioral studies (Greene and Zaidel, 2011 and Okada et al., 2012) is inconsistent, and thus, data from the IOG, STS, IPL, and IFG of both hemispheres (IOG: $x = \pm 36$, $y = -86$, $z = -8$; STS: $x = \pm 64$, $y = -46$, $z = 16$; IPL: $x = \pm 42$, $y = -48$, $z = 46$; IFG: $x = \pm 48$, $y = 24$, $z = 20$) were used by flipping ROIs in the right hemisphere based on MSP generation (cf. Henson et al., 2009). The parameters of the inversion were based on SPM default settings with the exception of not using a Hanning taper for the time series.

For every participant and condition, 3D source-reconstructed images in the MNI standard space of evoked activity were obtained every 50 ms between 0 and 400 ms in the post-stimulus window. The intensity was normalized to the mean over voxels and conditions to reduce inter-participant variance. All images were smoothed by 8 mm in the conversion from a cortical mesh to the MNI voxel space.

2.9.2 Difference.

The same method used for the commonality analysis was used to explore differences in brain activities in response to gaze and arrow cues. One exception was that the inverse reconstruction used to compute cortical source activities was restricted to other ROIs. Based on a previous fMRI study (Sato et al., 2009), three brain regions (the left-hemisphere SPL, the left-hemisphere PCG, and the right-hemisphere MTG) that showed different activation in response to gaze and arrow cues were selected. Another fMRI study also found differences in the MTG and the PCG (Hietanen et al., 2006). The center coordinates in both hemispheres were used for the SPL, PCG, and MTG (SPL: $x = \pm16$, $y = -52$, $z = 46$; PCG: $x = \pm32$, $y = 8$, $z = 42$; MTG: $x = \pm52$, $y = -66$, $z = 2$) by flipping ROIs in each hemisphere.

2.10 Data analysis: MEG regional brain activity analysis

2.10.1 Commonality.

The source-reconstruction images were entered into the random-effects general linear model (GLM) as repeated-measures factors including cue type (gaze vs. arrow), cue direction (directional vs. non-directional), and time window (0–50, 50–100, 100–150, 150–200, 200–250, 250–300, 300–350, and 350–400 ms); participant was a factor of no interest. The ensuing covariance components were estimated using a restricted maximum likelihood procedure to adjust the statistics. The low-variance regions, which can cause artificially high statistical values and localization bias, were also adjusted (Ridgway et al., 2012).

Planned contrasts were performed for each time window. Based on the objectives of the current study, the common activity associated with the effect of cue direction (directional vs. non-directional) across cue types (gaze and arrow) was tested using a conjunction analysis with interaction masking (Nichols et al., 2005 and Price and Friston, 1997; cf. Sato et al., 2009). First, the contrast of directional gaze versus non-directional gaze (contrast 1) and directional arrow versus non-directional arrow (contrast 2) was specified, and then the main effect of contrast 1 + 2 was exclusively masked by the *F*-tests of interactions (i.e., a two-tailed test of contrast 1 − contrast 2). The significance threshold of the masking was set to $p < 0.05$ (uncorrected). Significantly activated voxels were identified if they reached the extent threshold of 10 voxels with a height threshold of $p < 0.05$ (uncorrected). To display the activation, the root-mean-square (RMS) time course of MEG source activities within a 4-mm radius of the peak foci was extracted between 0 and 400 ms for each participant and averaged across participants.

Additionally, multiple regression analyses were performed to investigate the relationships between MEG source activity and behavioral measures, specifically RT. First, subtraction images between the directional and non-directional condition in each time window were created for each cue type. RT ratios between invalid and valid conditions were also calculated for each participant under gaze and arrow conditions and used as a measure of the cueing effect. This method allowed controlling for baseline RT difference across individuals to investigate the degree of attentional facilitation (c.f. Sereno and Holzman, 1996). Based on the results of the above conjunction analysis, we searched for voxels that showed a positive relationship between the source activity evoked by the directional cue and the cueing effect in the 200–250, 250–300, 300–350, and 350–400 ms time windows. Then, GLMs including the behavioral measure (cueing effect) as a covariate of interest and cue type (gaze and arrow) as a factor of interest were constructed; participant was a factor of no interest. To identify brain regions that exhibited the same relationship with the cueing effect under both gaze and arrow conditions, a conjunction analysis with interaction masking was conducted. The contrast of the positive regression slope with the cueing effect of gaze and arrow were masked by the *F*-tests of interactions (i.e., the differential regression slope between the cueing effect of gaze and arrow) in each time window. A significant activation was identified if the activation foci reached the height threshold of $p < 0.05$ with the extent threshold of 10 voxels.

Preliminary analyses were also conducted for target-related activities (cf. Nagata et al., 2012). However, we found that the MEG signals were severely contaminated by noise related to eye movements and hand responses to peripheral targets even after the ICA preprocessing. The results also showed effects around eye regions. Thus, we did not report the target-related activity in this paper.

2.10.2 Difference.

The same GLM used in the commonality analysis was used in this analysis. First, the contrasts between directional gaze and non-directional gaze (contrast 1) and between directional arrow and non-directional arrow (contrast 2) were specified. To explore the differences in brain activity in response to gaze and arrow cues, we analyzed the specific instances in which higher activity was more strongly associated with one stimulus type than with the other. For example, the interaction involving higher activity specifically for directional gaze was tested as follows: [(directional eyes − non-directional gaze) − (directional arrow − non-directional arrow)]. Significantly activated voxels were identified if they reached the extent threshold of 10 voxels with a height threshold of $p < .05$ (uncorrected).

3 Results

3.1. Behavioral performance

The RT results are presented in Fig. 3. The 2 (cue type) × 3 (cue-target validity) repeated-measures ANOVA for RT revealed a significant main effect of cue-target validity, indicating that RTs were shorter for valid cues compared with invalid and non-directional cues ($F(2, 24) = 20.96$, $p < 0.05$). The main effect of cue type ($F(1, 12) = 0.48$, $p > 0.1$) and the interaction between cue type and cue-target validity ($F(2, 24) = 0.75$, $p > 0.1$) were not significant. The multiple comparisons for the main effect of cue-target validity revealed that the RTs under the valid condition were shorter than were those under the invalid (t (24) = 5.89, $p < 0.05$) and non-directional (t (24) = 5.27, $p < 0.05$) conditions. Non-parametric Wilcoxon signed-rank tests confirmed significant differences between valid cues compared with invalid and non-directional cues ($Z > 3.10$, $p < 0.05$) as well the lack of significant differences between gaze and arrow cues under each validity condition ($Z < 0.25$, $p > 0.1$). The results revealed that participants exhibit cueing effects of comparable magnitudes in response to both gaze and arrow cues.

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Figure 3

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3.2. MEG: commonality

The inverse reconstruction to compute cortical source activities from MEG signals was conducted in eight predefined regions of interest (the IOG, STS, IPL, and IFG in both hemispheres). We analyzed 3D source-reconstructed images in the MNI standard space of cortical source activity. The common activity associated with the effect of cue direction (directional vs. non-directional) across cue types (gaze and arrow) was tested using a conjunction analysis with interaction masking. The main effect of cue direction, contrasting directional and non-directional cues, was tested for each 50-ms time window. Within the 0–50, 50–100, 100–150, and

150–200 ms time windows, no significant activations were observed. Significant activations were observed at 200–250 ms in the right STS region ($t(564) = 1.70$, $p = 0.04$; Fig. 4), at 250–300 ms in the left IFG ($t(564) = 2.44$, $p = 0.007$), at 300–350 ms in the bilateral IFG (left: $t(564) = 2.46$, $p = 0.007$; right $t(564) = 1.77$, $p = 0.038$) and the left STS ($t(564) = 1.81$, $p = 0.035$), and at 350–400 ms in the left STS region ($t(564) = 2.47$, $p = 0.007$) and the bilateral IFG (left: $t(564) = 1.90$, $p = 0.029$; right: $t(564) = 1.86$, $p = 0.035$).

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Figure 4

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Multiple regression analysis was performed to investigate the relationships between MEG source activity (the contrasts between the directional and non-directional conditions) and behavioral measures (RT ratios between invalid and valid conditions). Significant positive relationships were found at 200–250 ms with the left STS region ($t(22) = 1.88$, $p = 0.03$; Fig. 5) and the bilateral IFG (left: $t(22) = 2.58$, $p = 0.005$; right: $t(22) = 2.08$, $p = 0.019$); at 250–300 ms with the right IOG ($t(22) = 2.34$, $p = 0.01$) and the left IFG ($t(22) = 2.23$, $p = 0.013$); at 300–350 ms with the bilateral IOG (left: $t(22) = 2.27$, $p = 0.017$; right: $t(22) = 2.17$, $p =0.015$) and the left IFG ($t(22) = 1.79$, $p = 0.037$); and at 350–400 ms with the bilateral IOG (left: $t(22) = 1.92$, $p = 0.035$; right: $t(22) = 2.78$, $p = 0.005$).

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Figure 5

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3.3. MEG: difference

The inverse reconstruction to compute cortical source activities from MEG signals was conducted in six predefined ROIs (the SPL, PCG, and MTG in both hemispheres). We analyzed the specific instances in which higher activity was more strongly associated with one stimulus type than with the other. Significant activations were observed only in the 350–400 ms time window. The SPL in both hemispheres was activated in response to directional arrow cues (right: $t(564) = 1.82$, $p = 0.034$; left: $t(564) = 1.75$; $p = 0.039$, Fig.6), whereas the MTG in both hemispheres (right: $t(564) = 3.45$, $p < 0.001$; left: $t(564) = 2.58$; $p = 0.005$) and the left PCG ($t(564) = 1.81$; $p = 0.035$) was activated in response to directional gaze cues.

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Figure 6

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4 Discussion

The behavioral data from the present study demonstrate that participants localize cued targets more rapidly than they localize non-cued targets, irrespective of cue type. These results are consistent with previous findings indicating that both gaze (e.g., Friesen and Kingstone, 1998) and arrow (e.g., Tipples, 2002) cues automatically trigger attentional shifts. The participants analyzed in this study exhibited cueing effects of comparable magnitudes in response to both gaze and arrow cues. This allowed for the investigation of the neural substrates underlying the common behavioral response of attentional shifts induced by gaze and arrow cues.

The MEG data from the present study revealed a common activation for directional versus non-directional gaze and arrows in the STS and IFG. These spatial patterns are consistent with previous fMRI studies that indicate that directional gaze and arrows activate widespread temporoparietal and frontal regions (Sato et al., 2009 and Tipper et al., 2008). These results are also in line with the theoretical proposal that a neural network, which includes the STS and IFG, is associated with the reorienting of attention (Corbetta and Shulman, 2002) and suggest that the STS and the IFG perform the psychological process common to the attentional shifts induced by directional gaze and arrows.

Moreover, these MEG data revealed commonalities in the temporal profiles of this neural activation. First, directional versus non-directional cues commonly activated the right STS region at 200–250 ms. A visual inspection of this component (Fig. 4) indicates that the peak of this component occurred during the 150–200-ms time window, which is in line with several previous EEG and MEG studies using facial stimuli (e.g., Bentin et al., 1996; for a review, see Rossion and Jacques, 2008). The difference between cue directions at this component is also consistent with several EEG and MEG studies reporting higher amplitude for this component in response to an averted than to a straight gaze (Puce et al., 2000; Sato et al., 2008 and Watanabe et al., 2001). Hietanen et al. (2008) found that, in the cueing paradigm, both directional gaze and arrows induce larger amplitudes in this component than do non-directional cues. A previous combined fMRI and ERP study also reported that the amplitude of this component was correlated with BOLD signals in face-related regions including the STS (Horovitz et al., 2004). This result is also consistent with data from single-unit recording studies in monkeys that found that a subset of cells in the STS codes the direction of another's attention regardless of the visual features (Jellema et al., 2000 and Perrett et al., 1992) and with neuroimaging studies in humans that found that the STS was activated in response to different social attention signals including gaze (Hoffman and Haxby, 2000) and gestures (Sato et al., 2009). Together with these data, the current results suggest that the activation of the right STS region at 200–250 ms is involved in extracting directional information, irrespective of cue type.

Subsequently, after 250 ms, the focus of activation moved to the left IFG. The activation of the IFG in these time windows has also been shown by previous MEG studies. Nishitani et al. (2004) found that the left IFG was active at around 250 ms when participants observed and imitated another's mouth action. Sato et al. (submitted) demonstrated that dynamic versus static facial expressions activate the right IFG at 300–350 ms. Based on these findings, it would be reasonable to think that the information about cue direction processed by the right STS was transferred into the left IFG during this time window. It has been proposed that the STS and IFG are associated with the reorienting of attention by behaviorally relevant stimuli (Corbetta and Shulman, 2002). In our daily lives, the ability to react to the direction of gaze and arrows is highly relevant to the ability to effectively communicate with others (cf. Guzzon et al., 2010). Given that both factorial and regression analyses relate the overlapped left IFG activity to directional cues, this activation may be critical for attentional shifts induced by gaze and arrow cues.

The present findings also revealed the activation of the bilateral IFG and the left STS after 300 ms. Although the STS and IFG play an important role in orienting attention (e.g., Corbetta and Shulman, 2002), other studies have suggested that these brain regions are involved in various cognitive functions. For example, it has been proposed that the mirror neuron network, which includes the IFG and the STS, is employed in understanding the action intention of others (Rizzolatti et al., 2001). Previous fMRI studies suggest that the IFG and the STS play a role when inferring the intentions behind a symbolic gesture (Villarreal et al., 2012) and the animated motion of non-biological objects (Osaka et al., 2012 and Schultz et al., 2004). Behavioral studies also suggest that the inference of intention would be a critical component in attentional shifts induced by gaze and arrows. For example, some studies have shown that biological and non-biological cues did not trigger an attentional shift when the model's intention was ambiguous (Teufel et al., 2010 and Wiese et al., 2012). Based on these findings, the left STS activation and the prolonged activity of the bilateral IFG might function as a system that sustains or suppresses attentional shifts depending on whether information about intention is extracted from the cue.

The regression analysis also revealed that the activation of the STS and the IFG were positively correlated with the degree of the attentional shifts induced by gaze and arrow cues. We also found a positive relationship between the later activation (~250 ms) of the bilateral occipital cortex and the cueing effect. Previous EEG studies have reported that gaze and arrow cues trigger the enhancement of subsequent visual processing at occipitotemporal sites (Hopf and Mangun, 2000 and Schuller and Rossion, 2004). These findings suggest the possibility that the STS and the IFG send feedback signals to the visual cortex and enhance the visual processing of the subsequent target.

Spatial and temporal commonalities in the brain regions underlying the attentional shifts induced by gaze and arrows suggest that the human brain has incorporated the neural mechanisms for the processing of biological cues into those used for the processing of symbolic cues. Previous studies have shown that biological cues, including gaze, trigger attentional shifts even in macaque monkeys (Deaner and Platt, 2003). However, in addition to biological cues, symbolic representations of directional information, such as arrows (Sato et al., 2010) and words (i.e., right and left; Vecera and Rizzo, 2006), also trigger automatic attentional shifts in humans. Promising directions for further research include whether other attention-orienting cues (e.g., directional words) are also processed in the same manner and how spatial and temporal commonalities in the neural mechanisms underlying attentional shifts have developmentally and evolutionally emerged.

In contrast to our results showing common STS activation in response to gaze and arrow cues, some previous fMRI studies have reported different activation patterns in the STS in response to these cues (Hietanen et al. 2006 and Kingstone et al., 2004). Kingstone et al. (2004) found stronger STS activation in response to gaze than to other cues. They presented cue stimuli that could be perceived as eyes or as cars based on an instruction. This finding does not exclude the engagement of the STS during processing of other directional cues because cars do not inherently indicate the location of objects. Hietanen et al. (2006) found that gaze cues did not induce STS activation. In contrast to other studies (Sato et al., 2009, Tipper et al., 2008 and Kingstone et al., 2004), Hietanen et al. included no female participants. This may introduce ambiguity into the significance of STS activity in response to gaze cues, as women are more sensitive to the gaze of others than are men (see Frischen et al. (2007) for a review). In addition to these issues, these analyses differ from a methodological perspective. Previous studies (Hietanen et al. 2006 and Kingstone et al., 2004) performed separate contrasts for each cue and tested the difference in brain activity between gaze and arrow cues, whereas we performed statistical conjunction analyses to investigate the commonality from a positive perspective. This difference may explain the inconsistent results among the studies.

In addition to these areas of commonality, we also found differences in brain activity in response to gaze and arrow cues at the 350–400-ms time window. The results revealed that the SPL in both hemispheres was activated in response to directional arrow cues, whereas the MTG in both hemispheres and the left PCG was activated in response to directional gaze cues. Previous fMRI studies also demonstrated that arrow cues specifically activated the SPL (Hietanen et al., 2006 and Sato et al., 2009). Corbetta and Shulman (2002) proposed that the dorsal attention networks, including the SPL, were involved in top-down attention control, whereas the ventral attention networks were associated with stimulus-driven attention orienting. Several studies have shown that arrow cues trigger attentional shifts only when participants intend to follow the direction of the cues (e.g., Posner, 1980). These findings suggest that differences in brain activity may appear during later time windows, reflecting the stronger top-down control of attention induced by arrow than by gaze cues.

Several limitations of the current study should be acknowledged. First, although the functional roles of the STS and the IFG at each time window were discussed, the relationship between neural activation and the behavioral cueing effect addressed here was correlational rather than causal. The application of noninvasive transcranial stimulation methods could provide important information regarding whether the activation in specific brain regions in specific time windows is critical for automatic attention orienting by directional gaze and arrow cues. Second, this study did not find any activation of the IPL in response to directional gaze and arrow cues. This might relate to the fact that MEG has the disadvantage of being insensitive to deep or radially oriented sources (Dale and Sereno, 1993). Additional complementary methods with high spatial–temporal resolution (e.g., a combined EEG and fMRI study) would provide useful information concerning the neurocognitive mechanisms involved in attentional shifts induced by gaze and arrow cues. Third, some participants did not show reflexive attention orienting in response to gaze and arrow cues and were excluded from the MEG analysis. Several previous studies have shown that reflexive attention orienting clearly appeared at a shorter SOA (e.g., Langton and Bruce, 1999). Although we selected a relatively longer SOA to record a clear MEG signal without contamination by response-related activities, a shorter SOA may be useful for inducing robust reflexive attention orienting and underlying brain activation. Fourth, this study focused on cue-related and not target-related activity. A recent fMRI study comparing invalidly and validly cued targets demonstrated that arrow but not gaze cues recruited widely distributed brain regions including the STS, IPL, and IFG (Engell et al., 2010). Although eye movement and the response-related electromyogram to the peripherally presented target may contaminate the MEG signal, MEG would be useful for investigating the temporal characteristics of target-related activity in response to gaze and arrow cues.

5 Conclusions

The current study investigated the temporal dynamics of brain activation during attentional shifts induced by gaze and arrow cues. These findings demonstrate that both the STS and IFG are more activated in response to directional than non-directional gaze and arrow cues and that they exhibit a common temporal profile from 200–400 ms after cue onset. The regression analyses revealed that the activation of brain regions close to those specified in the factorial analysis (the STS and the IFG) and of the bilateral occipital cortex are positively correlated with the degree of the attentional shifts induced by gaze and arrow cues. We also found differences in brain activity in response to gaze and arrow cues at the 350–400-ms time window. The SPL in both hemispheres was activated in response to directional arrow cues, whereas the MTG in both hemispheres and the left PCG was activated in response to directional gaze cues. These results indicate commonalities and differences in the spatiotemporal neural dynamics underlying the attentional shifts by gaze and arrow cues.

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References

Bentin, S., Allison, T., Puce, A., Perez, E., McCarthy, G., 1996. Electrophysiological studies of face perception in humans. J. Cogn. Neurosci. 8, 551–565.

Brignani, D., Guzzon, D., Marzi, C.A., Miniussi, C., 2009. Attentional orienting induced by arrows and eye-gaze compared with an endogenous cue. Neuropsychologia 47, 370–381.

Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat. Rev. Neurosci. 3, 201–215.

Dale, A.M., Halgren, E., 2001. Spatiotemporal mapping of brain activity by integration of multiple imaging modalities. Curr. Opin. Neurobiol. 11, 202–208.

Dale, A., Sereno, M., 1993. Improved localization of cortical activity by combining EEG and MEG with MRI cortical surface reconstruction: a linear approach. J. Cogn. Neurosci. 5, 162–176.

Deaner, R.O., Platt, M.L., 2003. Reflexive social attention in monkeys and humans. Curr. Biol. 13, 1609–1613.

Driver, J., Davis, G., Ricciardelli, P., Kidd, P., Maxwell, E., Baron-Cohen, S., 1999. Gaze perception triggers reflexive visuospatial orienting. Vis. Cogn. 6, 509–540.

Emery, N.J., 2000. The eyes have it: the neuroethology, function and evolution of social gaze. Neurosci. Biobehav. Rev. 24, 581–604.

Engell, A.D., Nummenmaa, L., Oosterhof, N.N., Henson, R.N., Haxby, J.V., Calder, A.J., 2010. Differential activation of frontoparietal attention networks by social and symbolic spatial cues. Soc. Cogn. Affect. Neurosci. 5, 432–440.

Friesen, C.K., Kingstone, A., 1998. The eyes have it! Reflexive orienting is triggered by nonpredictive gaze. Psychon. Bull. Rev. 5, 490–495.

Friesen, C.K., Kingstone, A., 2004. Attentional effects of counterpredictive gaze and arrow cues. J. Exp. Psychol. Hum. Percept. Perform. 30, 319–329.

Frischen, A., Bayliss, A.P., Tipper, S.P., 2007. Gaze cueing of attention: visual attention, social cognition, and individual differences. Psychol. Bull. 133, 694–724.

Friston, K., Chu, C., Mourao-Miranda, J., Hulme, O., Rees, G., Penny, W., et al., 2008. Bayesian decoding of brain images. Neuroimage 39, 181–205.

Greene, D.J., Mooshagian, E., Kaplan, J.T., Zaidel, E., Iacoboni, M., 2009. The neural correlates of social attention: automatic orienting to social and nonsocial cues. Psychol. Res. 73, 499–511.

Greene, D.J., Zaidel, E., 2011. Hemispheric differences in attentional orienting by social cues. Neuropsychologia 49, 61–68.

Guzzon, D., Brignani, D., Miniussi, C., Marzi, C.A., 2010. Orienting of attention with eye and arrow cues and the effect of overtraining. Acta. Psychol. 134, 353–362.

Henson, R.N., Mouchlianitis, E., Friston, K.J., 2009. MEG and EEG data fusion: simultaneous localisation of face-evoked responses. Neuroimage 47, 581–589.

Hietanen, J.K., Leppanen, J. M., Nummenmaa, L., Astikainen, P., 2008. Visuospatial attention shifts by gaze and arrow cues: an ERP study. Brain Res. 1215, 123–136.

Hietanen, J.K., Nummenmaa, L., Nyman, M.J., Parkkola, R., Hamalainen, H., 2006. Automatic attention orienting by social and symbolic cues activates different neural networks: an fMRI study. Neuroimage 33, 406–413.

Hoffman, E.A., Haxby, J.V., 2000. Distinct representations of eye gaze and identity in the distributed human neural system for face perception. Nat. Neurosci. 3, 80–84.

Hommel, B., Pratt, J., Colzato, L., Godijn, R., 2001. Symbolic control of visual attention. Psychol. Sci. 12, 360–365.

Hopf, J.-M., Mangun, G.R., 2000. Shifting visual attention in space: an electrophysiological analysis using high spatial resolution mapping. Clin. Neurophysiol. 111, 1241–1257.

Horovitz, S.G., Rossion, B., Skudlarski, P., Gore, J.C., 2004. Parametric design and correlational analyses help integrating fMRI and electrophysiological data during face processing. Neuroimage 22, 1587–1595.

Jellema, T., Baker, C.I., Wicker, B., Perrett, D.I., 2000. Neural representation for the perception of the intentionality of actions. Brain Cogn. 44, 280–302.

Kingstone, A., Tipper, C., Ristic, J., Ngan, E., 2004. The eyes have it!: An fMRI investigation. Brain Cogn. 55, 269–271.

Langtone, S.R.H., Bruce, V., 1999. Reflexive visual orienting in response to the social attention of others. Vis. Cogn. 6, 541–567.

Litvak, V., Mattout, J., Kiebel, S., Phillips, C., Henson, R., Kilner, J., et al,. 2011. EEG and MEG data analysis in SPM8. Comput. Intell. Neurosci. 852961.

Mattout, J., Henson, R.N., Friston, K.J., 2007. Canonical source reconstruction for MEG. Comput. Intell. Neurosci. 67613.

Nagata Y., Bayless S.J, Mills T, Taylor M.J. 2012. Spatio–temporal localisation of attentional orienting to gaze and peripheral cues. Brain Res. 1439, 44–53.

Nichols, T., Brett, M., Andersson, J., Wager, T., Poline, J.B., 2005. Valid conjunction inference with the minimum statistic. Neuroimage 25, 653–660.

Nishitani, N., Avikainen, S., Hari, R., 2004. Abnormal imitation-related cortical activation sequences in Asperger's syndrome. Ann. Neurol. 55, 558–562.

Okada, T., Sato, W., Kubota, Y., Toichi, M., Murai, T., 2012. Right hemispheric dominance and interhemispheric cooperation in gaze-triggered reflexive shift of attention. Psychiatry Clin. Neurosci. 66, 97–104.

Oldfield, R.C., 1971. The assessment and analysis of handness: The Edinburgh inventory. Neuropsychologia 9, 97–113.

Osaka, N., Ikeda, T., Osaka, M., 2012. Effect of intentional bias on agency attribution of animated motion: an event-related fMRI study. PLoS One 7, e49053.

Perrett, D.I., Hietanen, J.K., Oram, M.W., Benson, P.J., 1992. Organization and functions of cells responsive to faces in the temporal cortex. Philos. Trans. R. Soc. Lond. B Biol. Sci. 335, 23–30.

Posner, M.I., 1980. Orienting of attention. Q. J. Exp. Psychol. 32, 3–25.

Price, C.J., Friston, K., 1997. Cognitive conjunction: a new approach to brain activation experiments. NeuroImage 5, 261–270.

Puce, A., Smith, A., Allison, T., 2000. ERPs evoked by viewing facial movements. Cogn. Neuropsych. 17, 221–239.

Ridgway, G.R., Litvak, V., Flandin, G., Friston, K.J., Penny, W.D., 2012. The problem of low variance voxels in statistical parametric mapping; a new hat avoids a 'haircut'. Neuroimage 59, 2131–2141.

Ristic, J., Wright, A., Kingstone, A., 2007. Attentional control and reflexive orienting to gaze and arrow cues. Psychon. Bull. Rev. 14, 964–969.

Rizzolatti, G., Fogassi, L., Gallese, V., 2001. Neurophysiological mechanisms underlying the understanding and imitation of action. Nat. Rev. Neurosci. 2, 661–670.

Rossion, B., Jacques, C., 2008. Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. Neuroimage 39, 1959–1979.

Sato, W., Kochiyama, T., Uono, S., Yoshikawa, S., 2008. Time course of superior temporal sulcus activity in response to eye gaze: a combined fMRI and MEG study. Soc. Cogn. Affect. Neurosci. 3, 224–232.

Sato, W., Kochiyama, T., Uono, S., Yoshikawa, S., 2009. Commonalities in the neural mechanisms underlying automatic attentional shifts by gaze, gestures, and symbols. Neuroimage 45, 984–992.

Sato, W., Kochiyama, T., Uono, S., Yoshikawa, S., 2010. Automatic attentional shifts by gaze, gaztures, and symbols. Psychologia 53, 27–35.

Sato, W., Okada, T., Toichi, M., 2007. Attentional shift by gaze is triggered without awareness. Exp. Brain Res. 183, 87–94.

Schuller, A.M., Rossion, B., 2004. Perception of static eye gaze direction facilitates subsequent early visual processing. Clin. Neurophysiol. 115, 1161–1168.

Schultz, J., Imamizu, H., Kawato, M., Frith, C.D., 2004. Activation of the human superior temporal gyrus during observation of goal attribution by intentional objects. J. Cogn. Neurosci. 16, 1695–1705.

Sereno, A.B., Holzman, P.S., 1996. Spatial selective attention in schizophrenic, affective disorder, and normal subjects. Schizophr. Res. 20, 33-50.

Stevens, S.A., West, G.L., Al-Aidroos, N., Weger, U.W., Pratt, J., 2008. Testing whether gaze cues and arrow cues produce reflexive or volitional shifts of attention. Psychon. Bull. Rev. 15, 1148–1153.

Teufel, C., Alexis, D. M., Clayton, N.S., Davis, G., 2010. Mental-state attribution drives rapid, reflexive gaze following. Atten. Percept. Psychophys. 72, 695–705.

Tipper, C.M., Handy, T.C., Giesbrecht, B., Kingstone, A., 2008. Brain responses to biological relevance. J. Cogn. Neurosci. 20, 879–891.

Tipples, J., 2002. Eye gaze is not unique: automatic orienting in response to uninformative arrows. Psychon. Bull. Rev. 9, 314–318.

Tipples, J., 2008. Orienting to counterpredictive gaze and arrow cues. Percept. Psychophys. 70, 77–87.

Vecera, S.P., Rizzo, M., 2006. Eye gaze does not produce reflexive shifts of attention: evidence from frontal-lobe damage. Neuropsychologia 44, 150–159.

Villarreal, M.F., Fridman, E.A., Leiguarda, R.C., 2012. The effect of the visual context in the recognition of symbolic gestures. PLoS One 7, e29644.

Watanabe, S., Kakigi, R., Puce, A., 2001. Occipitotemporal activity elicited by viewing eye movements: a magnetoencephalographic study. Neuroimage 13, 351–363.

Wiese, E., Wykowska, A., Zwickel, J., Muller, H.J., 2012. I see what you mean: how attentional selection is shaped by ascribing intentions to others. PLoS One 7, e45391.

Figure Legends

Figure 1 Examples of gaze and arrow stimuli.

Figure 2 Sequence of stimulus presentation under the invalid condition.

Figure 3 Mean (with *SE*) reaction times to localize the target.

Figure 4 Common brain activation in response to directional versus non-directional gaze and arrow cues in each time window. The height threshold of $p < 0.05$ (uncorrected) with the extent threshold of 10 voxels. Waveforms represent source estimates in response to directional and non-directional gaze and arrow cues in the ROIs. Error bars show the *SE*.

Figure 5 Common brain regions showing a positive relationship between the cueing effect and the activation to directional versus non-directional gaze and arrow cues in each time window. The height threshold of $p < 0.05$ (uncorrected) with the extent threshold of 10 voxels. RT ratios between invalid and valid conditions were also calculated for each participant under gaze and arrow conditions and used as a measure of the cueing effect. The cueing effect is plotted against contrasts between the directional and non-directional conditions in the ROIs. Solid and broken lines represent linear regressions in gaze and arrow cues, respectively.

Figure 6 The brain regions showing different activation in response to directional versus non-directional gaze and arrow cues at 350–400 ms. The height threshold is $p < 0.05$ (uncorrected), and the extent threshold is 10 voxels. Waveforms represent source estimates in response to directional and non-directional gaze and arrow cues in the ROIs. Error bars show the *SE*.

Figure 1

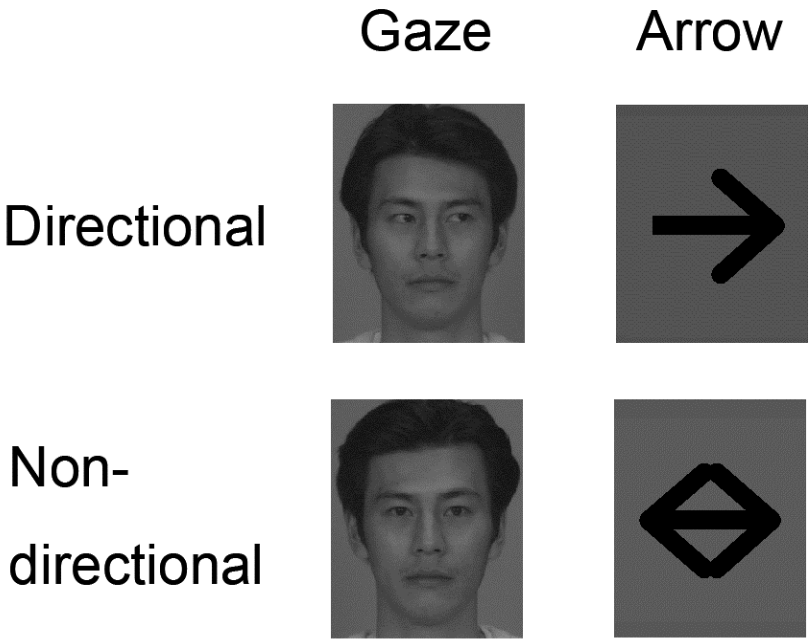


Figure 2

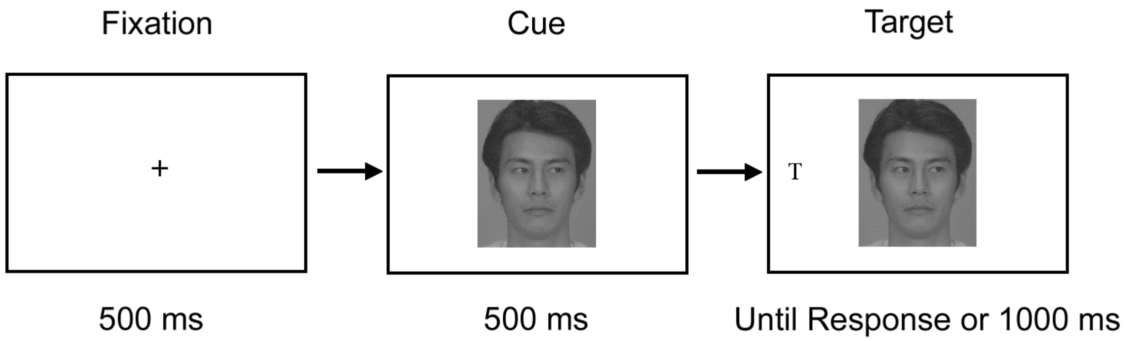
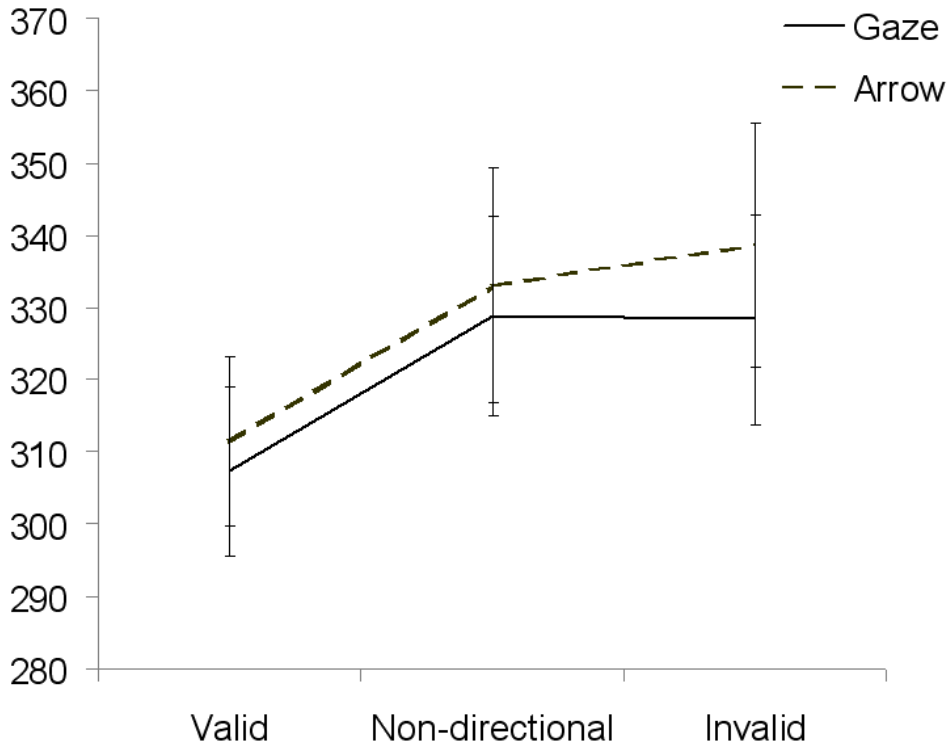


Figure 3


370
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350
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330
320
310
300
290
280
Gaze
Arrow
Valid
Non-directional
Invalid

Figure 4

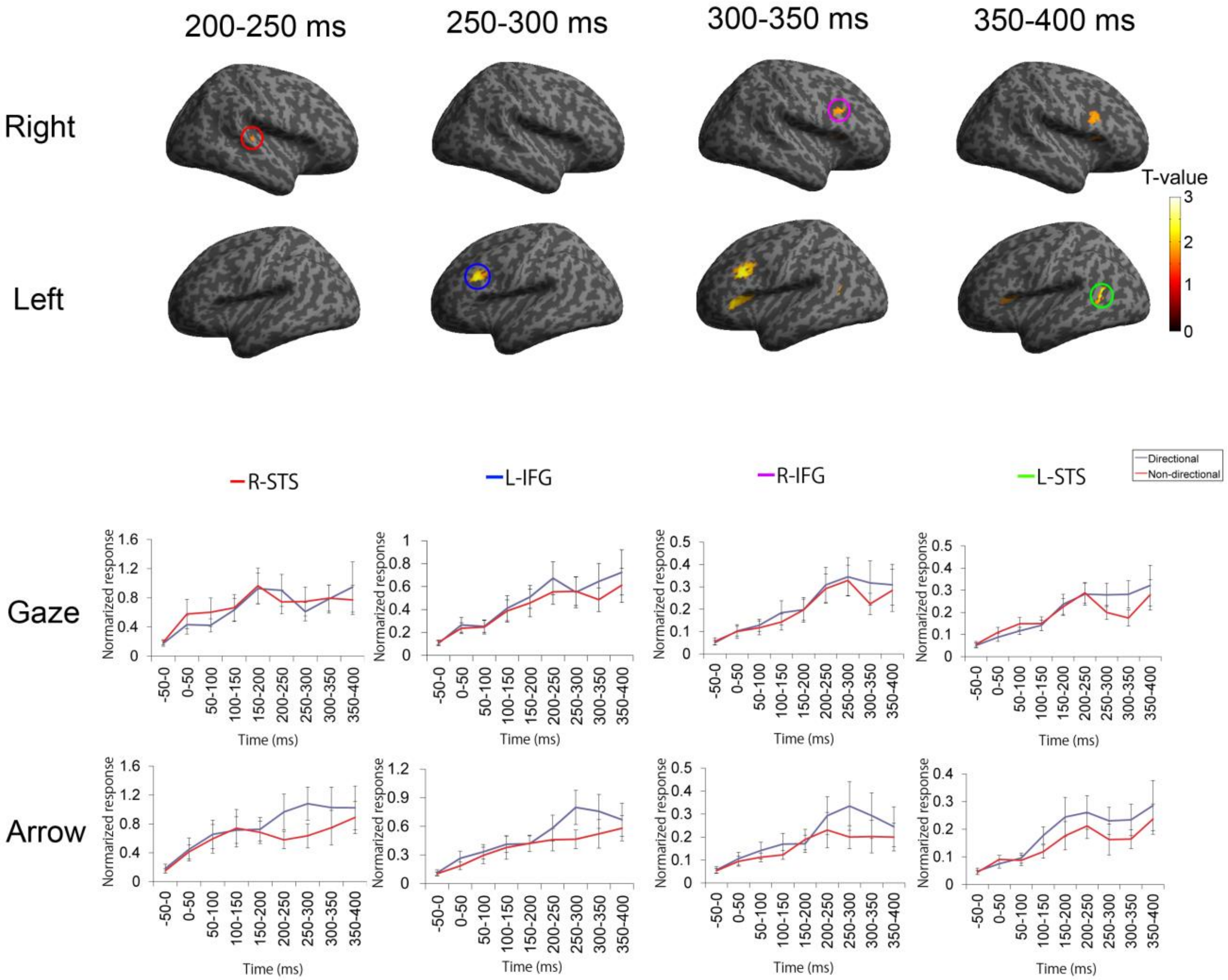
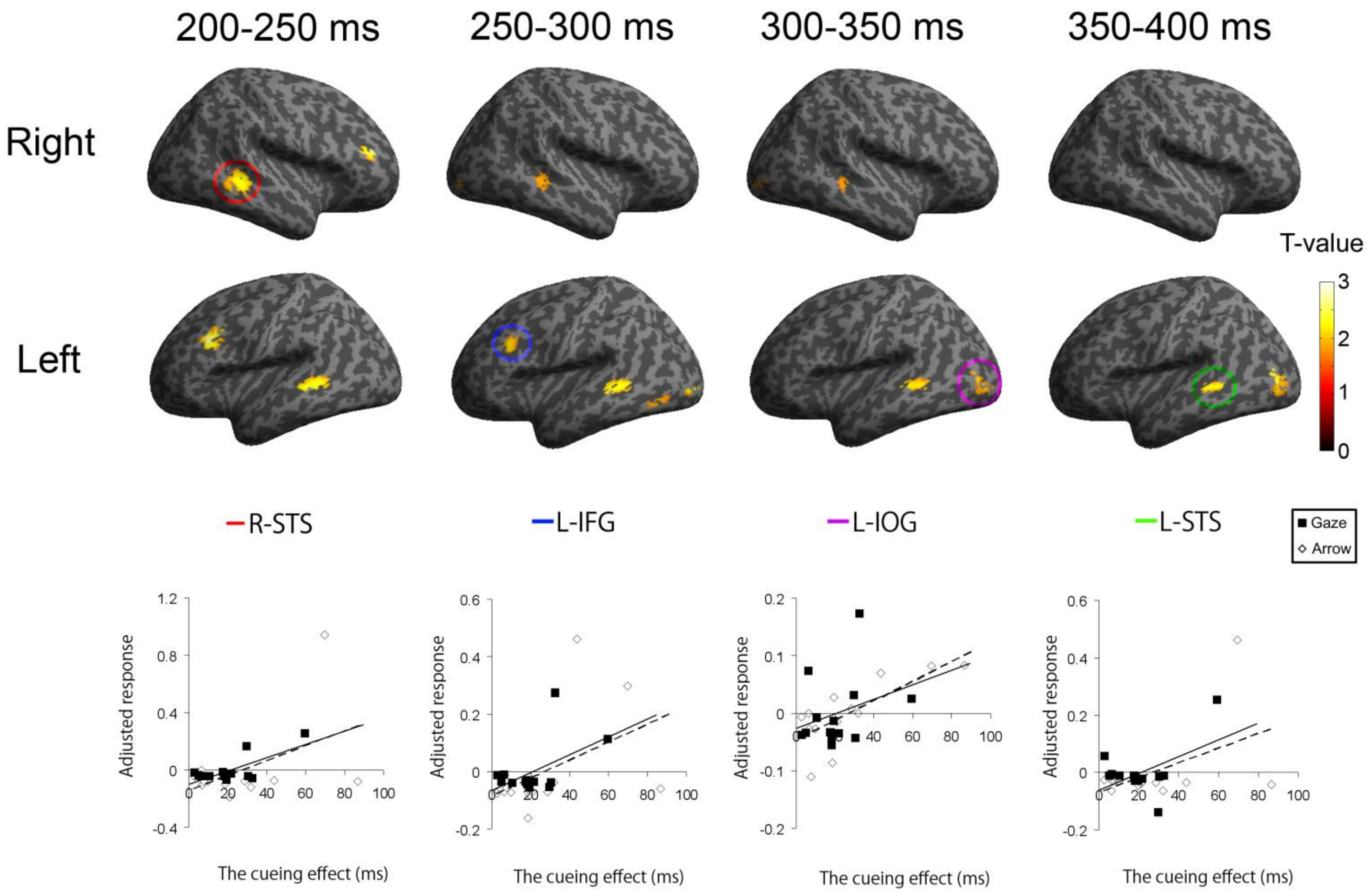

200-250 ms
250-300 ms
300-350 ms
350-400 ms
Right
Left
T-value
3
2
1
0
R-STS
L-IFG
R-IFG
L-STS
Directional
Non-directional
Gaze
Arrow
Normarized response
Time (ms)
-50-0
0-50
50-100
100-150
150-200
200-250
250-300
300-350
350-400

Figure 5


200-250 ms
250-300 ms
300-350 ms
350-400 ms
Right
Left
T-value
3
2
1
0
R-STS
L-IFG
L-IOG
L-STS
Gaze
Arrow
Adjusted response
The cueing effect (ms)
1.2
0.8
0.4
0
-0.4
0.6
0.4
0.2
0
-0.2
0.2
0.1
0
-0.1
-0.2
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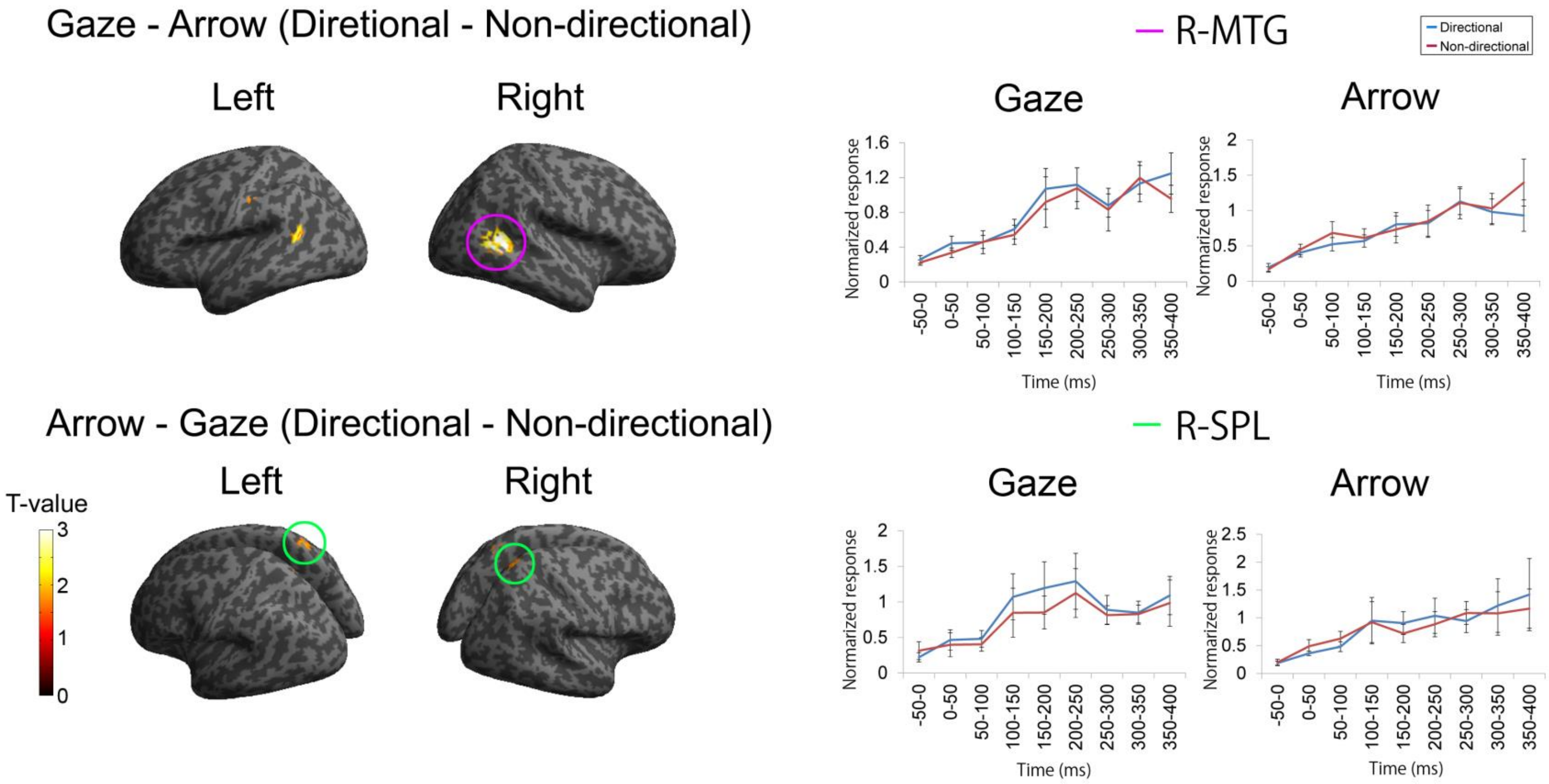
40
60
80
100

857 Figure 6



858