Neuroscience Research 87 (2014) 56–65

Contents lists available at ScienceDirect

Neuroscience Research

journal homepage: www.elsevier.com/locate/neures

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

Shota Uono[a,*], Wataru Sato[b], Takanori Kochiyama[b]

[a] *Graduate School of Education, Kyoto University, Yoshida-honmachi, Sakyo-ku, Kyoto 606-8501, Japan*
[b] *The Hakubi Project, Primate Research Institute, Kyoto University, Inuyama, Aichi 484-8506, Japan*

ARTICLE INFO

Article history:
Received 29 October 2013
Received in revised form 3 June 2014
Accepted 8 July 2014
Available online 23 July 2014

Keywords:
Attention orienting
Arrow
Gaze
Magnetoencephalography (MEG)

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.

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; 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; Tipples, 2008). These studies found that both types of cues trigger attentional shifts even when they are counterpredictive of target

---

* Corresponding author. Current address: Graduate School of Medicine, Faculty of Human Health Science, Kyoto University, 53 Shogoin-Kawaharacho, Sakyo-ku, Kyoto 606-8507, Japan. Tel.: +81 75 753 3067; fax: +81 75 753 3067.
E-mail address: uonoshota1982@gmail.com (S. Uono).

http://dx.doi.org/10.1016/j.neures.2014.07.003
0168-0102/

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; 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; 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; 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; 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; 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; Ristic et al., 2007) and fMRI (Hietanen et al., 2006; Tipper et al., 2008; 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, 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