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Spatiotemporal commonalities of fronto-parietal activation in attentional orienting triggered by supraliminal and subliminal gaze cues: An event-related potential study

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ABSTRACT

Eye gaze triggers attentional shifts with and without conscious awareness. It remains unclear whether the spatiotemporal patterns of electric neural activity are the same for conscious and unconscious attentional shifts. Thus, the present study recorded event-related potentials (ERPs) and evaluated the neural activation involved in attentional orienting induced by subliminal and supraliminal gaze cues. Nonpredictive gaze cues were presented in the central field of vision, and participants were asked to detect a subsequent peripheral target. The mean reaction time was shorter for congruent gaze cues than for incongruent gaze cues under both presentation conditions, indicating that both types of cues reliably trigger attentional orienting. The ERP analysis revealed that averted versus straight gaze induced greater negative deflection in the bilateral fronto-central and temporal regions between 278 and 344 ms under both supraliminal and subliminal presentation conditions. Supraliminal cues, irrespective of gaze direction, induced a greater negative amplitude than did subliminal cues at the right posterior cortices at a peak of approximately 170 ms and in the 200–300 ms. These results suggest that similar spatial and temporal fronto-parietal activity is involved in attentional orienting triggered by both supraliminal and subliminal gaze cues, although inputs from different visual processing routes (cortical and subcortical regions) may trigger activity in the attentional network.

1. Introduction

Gaze processing is a critical aspect of human social cognition. We are able to extract important information from another's gaze direction, including information about that individual's attentional focus and mental state, and this information may help us to respond appropriately to subsequent events (Emery, 2000). Behavioral studies have shown that humans are highly sensitive to the gaze direction of others (Symons, Lee, Cedrone, & Nishimura, 2004; Uono & Hietanen, 2015), and orient their attention in the direction of the gaze of another (Frischen, Bayliss, & Tipper, 2007 for a review). For example, Friesen and Kingstone (1998) investigated the attentional effects of gaze cues that were nonpredictive of the location of a subsequent target. Participants were instructed to respond to targets that appeared either to the left or right side of the face upon which the gaze cues were presented. The results showed that reaction times (RTs) in the gaze-at-target (i.e., congruent gaze cue) condition were shorter than those in the non-gaze-at-target (i.e., incongruent gaze cue) condition, indicating that gaze cues reflexively trigger attentional orienting.

Recent behavioral studies have further revealed that eye gaze information triggers attentional orienting even when observers are not aware of the existence of the gaze-cue stimuli (Al-Janabi & Finkbeiner, 2012; Bailey et al., 2014; Mitsuda and Masaki, 2018; Sato, Kochiyama, Uono, & Toichi, 2016; Sato, Okada, & Toichi, 2007; Tokunaga & Miyatani, 2010; Xu, Zhang, & Geng, 2011). The attentional effects of both subliminally and supraliminally presented gaze emerges even when the direction of the gaze is not predictive of the target location (Bailey et al., 2014; Sato et al., 2007; Tokunaga & Miyatani, 2010) and under heavy perceptual load (Xu et al., 2011). These studies suggest that subliminal and supraliminal gaze cues share the characteristic of automatically induced attentional orienting. However, studies that have investigated specific populations have shown differences in the patterns of attentional orienting observed with supraliminal versus subliminal gaze cues. A reduced gaze cueing effect has been observed

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under subliminal presentation among individuals with autism spectrum disorder (ASD) (Sato, Uono, Okada, & Toichi, 2010) and under supraliminal presentation among older adults compared to controls (Bailey et al., 2014). This dissociation suggests the involvement of different mechanisms of attentional orienting in the processing of these two types of gaze cues.

For theoretical and clinical reasons, it is desirable to have an understanding of whether the same or different mechanisms underlie attentional orienting in response to supraliminal and subliminal gaze cues. Several studies have investigated the neural mechanisms of gaze processing within the framework of the cueing paradigm. These studies have consistently demonstrated that temporal, parietal, and frontal regions are involved in attentional orienting triggered by supraliminal gaze cues (Callejas, Shulman, & Corbetta, 2014; Greene, Mooshagian, Kaplan, Zaidel, & Iacoboni, 2009; Sato, Kochiyama, Uono, & Yoshikawa, 2009; Tipper, Handy, Giesbrecht, & Kingstone, 2008). The activated brain regions include the posterior visual cortices, including the superior and middle temporal cortex (the superior temporal sulcus [STS] region), which is related to the visual processing of gaze direction (e.g., Hoffman & Haxby, 2000), and the attentional network, which includes the inferior parietal lobule (IPL) and the inferior/middle frontal gyrus (IFG/MFG) (cf. Vossel, Geng, & Fink, 2014). Furthermore, connectivity analyses have suggested that these regions constitute a functional network in gaze-triggered attentional orienting (Callejas et al., 2014; Lockhofen, Gruppe, Ruprecht, Gallhofer, & Sammer, 2014; Nummenmaa, Passamonti, Rowe, Engell, & Calder, 2010). Importantly, a recent functional magnetic resonance imaging (fMRI) study directly compared the brain activation involved in attentional orienting to supraliminal and subliminal gaze cues (Sato et al., 2016). Consistent with the findings of behavioral studies showing similar patterns for both types of cues (e.g., Sato et al., 2007), this study found that frontal, parietal, and temporal regions, including the STS region, the IPL, and the MFG, were activated more strongly in response to averted gaze relative to straight gaze, and that this effect occurred under both supraliminal and subliminal presentation. The study also found distinct brain regions associated with attentional orienting to supraliminal versus subliminal gaze cues. While supraliminal averted gaze specifically induced activation in the parietal lobe, subliminal averted gaze elicited activation in the frontal and temporal cortices and in subcortical regions such as the amygdala. These findings suggest that both common and distinct neurocognitive mechanisms are involved in attentional orienting to supraliminal and subliminal gaze cues.

Electrophysiological recording at a high temporal resolution offers a promising method for investigating whether the spatiotemporal patterns of neural activation involved in attentional orienting differ between supraliminal and subliminal gaze cues. With regard to supraliminal gaze, several electroencepharography (EEG) and magnetoencepharography (MEG) studies have shown that, compared to straight gaze, averted gaze induces a relatively greater amplitude with respect to the face-specific response at the right occipito-temporal site at approximately 170 ms after stimulus onset (Itier, Alain, Kovacevic, & McIntosh, 2007; Puce, Smith, & Allison, 2000; Sato, Kochiyama, Uono, & Yoshikawa, 2008; Watanabe, Kakigi, & Puce, 2001); however, other studies have reported no sensitivity to gaze direction in the corresponding component (e.g., Klucharev & Sams, 2004; McCarthy, Puce, Belger, & Allison, 1999; Schweinberger, Kloth, & Jenkins, 2007; Taylor, Itier, Allison, & Edmonds, 2001). In the cueing paradigm, differential neural activity was also found for averted versus straight gaze in fronto-parietal regions at a later temporal window. An event-relate potential (ERP) study reported differences in electrical activity between averted and straight gaze at the central and parietal sites within a temporal window of 200–500 ms after stimulus onset (Hietanen, Leppänen, Nummenmaa, & Astikainen, 2008). An MEG study demonstrated that both the posterior STS and IFG were more activated for averted gaze than for straight gaze cues between 200 and 400 ms after stimulus onset (Uono et al., 2014). These findings suggest that the perceptual processing of gaze direction occurs within the temporal cortex (at approximately 200 ms post-stimulus onset) and that the processed information is projected into fronto-parietal regions, triggering attentional orienting (after 200 ms). A recent ERP study investigating subliminally presented gaze stimuli demonstrated that unseen straight versus averted gaze induced a greater degree of negative deflection at frontoparietal electrodes after 200–350 ms during a gaze discrimination task performed under continuous flash suppression (Yokoyama, Noguchi, & Kita, 2013). This pattern of ERPs differed from those of the abovementioned studies, which reported enhanced activity in response to supraliminal averted gaze versus straight gaze cues under the attentional cueing paradigm. Although the different patterns of activation might have been due to different processing mechanisms for supraliminal and subliminal stimuli, task demand may have also had an effect. For example, the attentional cueing paradigm might bias an individual to process directional cues (i.e., averted gaze) relevant to the target location compared to the other paradigm (e.g., gaze direction discrimination). Thus, to clarify the neural correlates of attention orienting triggered by supraliminal and subliminal gaze cues, the present study compared ERP responses to subliminal and supraliminal averted versus straight gaze cues using an attentional cueing paradigm.

The present study used ERPs to investigate the commonalities and differences in neural activity between attentional orienting to subliminal and supraliminal gaze cues. Participants observed averted- and straight-gaze stimuli presented supraliminally or subliminally in the central visual field, and then detected a subsequent peripheral target. Reaction times (RT) for target detection were analyzed to confirm that gaze cues under both presentation conditions triggered attention orienting to the cued direction by comparing RTs under the congruent condition to RTs under the other cue conditions (non-cued and incongruent). ERP analyses were conducted to determine whether the supraliminal and subliminal directional cues that triggered attention orienting were processed differently (cf. Sato et al., 2016, Sato, Kochiyama, Uono, Yoshimura, & Toichi, 2017; Uono et al., 2014). The ERP data were analyzed using a 3D space–time SPM approach (Kilner & Friston, 2010; Litvak et al., 2011), which allows for the sensitive spatiotemporal localization of experimental effects while controlling for multiple comparisons of latencies and electrodes. Based on previous fMRI and electrophysiological studies, it was predicted that activity in the fronto-parietal regions after 200 ms would display common and distinct temporal profiles for the supraliminal and subliminal presentations. First, we conducted a cognitive conjunction analysis (Price & Friston, 1997) to identify commonalities in neural activity in response to averted (right and left) versus straight gaze across presentation conditions (supraliminal and subliminal). Second, we examined whether the neural activity in fronto-parietal regions showed distinct spatiotemporal patterns between the two types of gaze cues by analyzing the interaction between gaze direction and presentation. Additionally, we investigated the effects of supraliminal and subliminal presentation. A recent ERP study showed that seen faces induced a greater negative amplitude in a face-specific component (N170: Bentin, Allison, Puce, Perez, & McCarthy, 1996) relative to unseen faces specifically at the right occipito-temporal site (Navajas, Ahmadi, & Quian Quiroga, 2013). Other ERP studies have demonstrated that the conscious perception of faces is also associated with a greater negative amplitude within the 200–300 ms window at the right posterior site (Genetti, Britz, Michel, & Pegna, 2010; Pegna, Darque, Berrut, & Khateb, 2011). Therefore, we hypothesized that the supraliminal presentation of gaze cues would induce greater negative deflection relative to subliminal presentation at the posterior electrode (P8) at approximately 170 ms and within the 200–300 ms temporal window.