



Neural mechanisms underlying conscious and unconscious attentional shifts triggered by eye gaze



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ABSTRACT

Behavioral studies have shown that eye gaze triggers attentional shifts both with and without conscious awareness. However, the neural substrates of conscious and unconscious attentional shifts triggered by eye gaze remain unclear. To investigate this issue, we measured brain activity using event-related functional magnetic resonance imaging while participants observed averted or straight eye-gaze cues presented supraliminally or subliminally in the central visual field and then localized a subsequent target in the peripheral visual field. Reaction times for localizing the targets were shorter under both supraliminal and subliminal conditions when eye-gaze cues were directionally congruent with the target locations than when they were directionally neutral. Conjunction analyses revealed that a bilateral cortical network, including the middle temporal gyri, inferior parietal lobules, anterior cingulate cortices, and superior and middle frontal gyri, was activated more in response to averted eyes than to straight eyes under both supraliminal and subliminal conditions. Interaction analyses revealed that the right inferior parietal lobule was specifically active when participants viewed averted eyes relative to straight eyes under the supraliminal condition; the bilateral subcortical regions, including the superior colliculus and amygdala, and the middle temporal and inferior frontal gyri in the right hemisphere were activated in response to averted versus straight eyes under the subliminal condition. These results suggest commonalities and differences in the neural mechanisms underlying conscious and unconscious attentional shifts triggered by eye gaze.

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Introduction

The eyes of other individuals automatically trigger multiple psychological activities in observers (Kendon, 1967). For example, the perception of averted eyes may alert observers to critical information about the environment, such as dangerous animals, and allow rapid reactions to such stimuli. At the same time, averted eyes may signal the intention to share attentional focus with others and thereby create social coordination.

Consistent with these ideas, several behavioral studies have revealed that eye gaze can trigger attentional shifts under both conscious and unconscious conditions (Al-Janabi and Finkbeiner, 2012; Bailey et al., 2014; Sato et al., 2007, 2010; Xu et al., 2011). In these studies, researchers presented eye-gaze cues in the central visual field either supraliminally or subliminally using a cueing paradigm (cf. Posner, 1980). The results consistently showed that participants' reaction times (RTs) for processing targets were shorter when the targets were

preceded by cues that were directionally congruent with the target locations than when they were preceded by directionally incongruent cues under both presentation conditions. This cueing effect was observed under both supraliminal and subliminal presentation conditions when the cues were not predictive of target locations (Bailey et al., 2014; Sato et al., 2007, 2010; Xu et al., 2011; however, see Al-Janabi and Finkbeiner, 2012) and when concurrent information load was high (Xu et al., 2011). These data suggest that attentional shifts are automatically triggered by eyes, following a common pattern with and without conscious awareness. At the same time, some of these studies found different patterns of attentional shifts across supraliminal and subliminal presentation conditions. Specifically, reduced cueing effects caused by eye cues were found under subliminal, but not supraliminal, conditions among individuals with autistic spectrum disorders compared with typically developing controls (Sato et al., 2010) and under supraliminal, but not subliminal, conditions in older adults relative to younger adults (Bailey et al., 2014). These dissociations suggest the involvement of different mechanisms in conscious and unconscious gaze-triggered attentional shifts. In summary, behavioral data suggest that both conscious and unconscious viewing of eyes can trigger attentional shifts, with certain commonalities and differences evident across conditions.

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Neuroimaging studies have explored the neural mechanisms underlying attentional shifts triggered by consciously viewed eye gaze. A number of studies reported that the observation of averted eyes compared with straight eyes or other control stimuli, elicited more activation in several brain regions, including the posterior superior temporal sulcus/middle temporal gyrus (Calder et al., 2002; Engell and Haxby, 2007; Hoffman and Haxby, 2000; Hooker et al., 2003; Pelphrey et al., 2003; Puce et al., 1998; Sato et al., 2008; Wicker et al., 1998), fusiform gyrus (Calder et al., 2002; George et al., 2001; Pelphrey et al., 2003; Wicker et al., 1998), inferior parietal lobule (Calder et al., 2002; Hoffman and Haxby, 2000; Pelphrey et al., 2003; Sato et al., 2008; Wicker et al., 1998), and middle/inferior frontal gyrus (Calder et al., 2002; Hooker et al., 2003; Wicker et al., 1998). Several studies investigated the brain activation in response to averted versus straight eyes in the framework of the cueing paradigm (Callejas et al., 2013; Cazzato et al., 2012; Engell et al., 2010; Greene et al., 2009; Hietanen et al., 2006; Kingstone et al., 2004; Sato et al., 2009; Tipper et al., 2008). Although foci, methodologies, and results were not identical across these studies and disagreements persist, several of these studies (Greene et al., 2009; Sato et al., 2009; Tipper et al., 2008) were consistent in reporting that the temporal, parietal, and frontal regions were involved in attentional shifts triggered by eye gaze. For example, Tipper et al. (2008) presented eye-gaze cues using a cueing paradigm and found activation in the distributed temporal, parietal, and frontal regions, including the superior temporal gyrus, inferior parietal lobule, and middle and inferior frontal gyri, during attentional shifts elicited by eye-gaze cues. Several neuroimaging studies also reported that these regions were active when attentional shifts were automatically triggered by non-social cues, such as peripheral sudden onset stimuli and centrally presented symbols (e.g., Rosen et al., 1999; for a review, see Grosbras et al., 2005). Several studies reported that similar brain regions were activated for attentional shifts, regardless of whether they were triggered by eye gaze or non-social cues (Greene et al., 2009; Sato et al., 2009; Tipper et al., 2008; however, see Hietanen et al., 2006). Based on this evidence, it has been proposed that these regions constitute the attentional neural network (Corbetta and Shulman, 2002; Grosbras et al., 2005). Taken together, these findings suggest that conscious attentional shifts induced by gaze are implemented by the activation of the temporo-parieto-frontal cortical attentional network.

However, questions about whether the neural mechanisms underlying attentional shifts triggered by consciously and unconsciously perceived gaze could be common or different remain unanswered. No study has examined this issue. However, the aforementioned behavioral data showing commonalities across conscious and unconscious gaze-triggered attentional shifts suggest commonalities in the neural substrates. Several neuroimaging studies also reported common patterns in neural activation regarding the conscious and unconscious processing of facial stimuli (Jiang and He, 2006; Morris et al., 2007; Prochnow et al., 2013). Based on these data, we hypothesized that the temporo-parieto-frontal attentional network would be involved in both conscious and unconscious gaze-triggered attentional shifts.

Additionally, based on the behavioral data, we expected to find several differences between conscious and unconscious gaze-triggered attentional shifts. Neuroimaging studies have provided indirect evidence related to this issue, reporting that the amygdala was involved in the processing of subliminally presented facial stimuli (e.g., Morris et al., 1998; Whalen et al., 1998) and specifically activated in response to subliminally presented fearful versus neutral eyes (Whalen et al., 2004). A neuroimaging study reported that the activity of the amygdala of a patient with damage to the entrance of the cortical visual areas changed depending on the direction of unseen eyes (Burra et al., 2013). An intracranial electroencephalography study reported that amygdala activation in response to eyes was rapid, indicating that it can occur prior to or simultaneously with the conscious awareness of faces (Sato et al., 2011, 2013). Several neuroimaging studies also found that emotional facial expressions, which are integratively

processed with gaze direction (e.g., Sato et al., 2004), were unconsciously processed through the subcortical visual pathway to the amygdala, which includes the superior colliculus and pulvinar (e.g., Morris et al., 2001; for a review, see Tamietto and de Gelder, 2010). Further, the visual pathways involved in processing conscious and unconscious emotional facial expressions differed (e.g., Vuilleumier et al., 2002; for a review, see Vuilleumier and Pourtois, 2007). These data suggest the involvement of subcortical structures in the unconscious processing of eyes. Although direct evidence is lacking, based on these studies together with behavioral data suggesting specific mechanisms for unconscious gaze-triggered attentional shifts, we hypothesized that subcortical structures would be specifically related to unconscious attentional shifts triggered by gaze.

To test these hypotheses, we measured brain activity using rapid event-related functional magnetic resonance imaging (fMRI) while participants observed averted and straight eyes presented supraliminally or subliminally in the central visual field and then localized a subsequent target in the peripheral visual field. We performed cognitive conjunction analysis with interaction masking (Price and Friston, 1997) to identify commonalities in brain activity in response to averted versus straight eyes across presentation conditions. We also examined differences in brain activity by analyzing interactions between gaze direction and presentation condition.

Methods

Participants

Twenty-seven volunteers (3 women and 24 men; mean \pm SD age, 25.0 \pm 4.6 years) participated in the experiment. All participants were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971), and had normal or corrected-to-normal visual acuity. After the experimental procedures were fully explained, all participants provided informed consent regarding their participation. This study was approved by the local institutional ethics committee.

Experimental design

The fMRI analysis relied on a within-subject two-factorial design, including presentation condition (subliminal or supraliminal) and directional condition (averted or straight). Cue-target congruence (i.e., congruence between the cue's direction and the target's location: congruent, neutral, incongruent) was also included in the behavioral data analysis.

Stimuli

The eye-gaze stimuli were almost identical to those used in a previous behavioral study (Uono et al., 2009) (Fig. 1). We selected the cue stimuli from a standard set (Ekman and Friesen, 1976). Photographs of two models (one female and one male) showing a neutral facial expression were selected and manipulated. To manipulate gaze direction, the irises and pupils of the eyes were extracted from the original photographs and inserted at the right or left side of the eyeball using Adobe Photoshop 5.0. We cropped the photographs in an elliptical shape, 2.7° wide and 3.8° high, to exclude hair and background.

A mosaic image was created from a neutral facial expression by dividing the photos into a 50 \times 40 grid and randomly reordering the pieces, rendering the resulting photograph unrecognizable as a face. The letter "T" (0.6° wide \times 0.6° high), presented 5.7° to the left or right of the center of the screen, was used as a target stimulus.

Presentation apparatus

The events were controlled by Presentation Software version 10.0 (Neurobehavioral Systems, Albany, CA, USA) implemented on a computer

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