

The role of the oculomotor system in covert social attention

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Abstract Observing a change in gaze direction triggers a reflexive shift of attention and appears to engage the eye-movement system. However, the functional relationship between social attention and this oculomotor activation is unclear. One extremely influential hypothesis is that the preparation of a saccadic eye movement is necessary and sufficient for a covert, reflexive shift of attention (the *premotor* theory of attention; Rizzolatti et al., 1994). Surprisingly, this theory has not been directly tested with respect to reflexive gaze cueing. In order to address this issue, gaze cueing, peripheral cueing, and arrow cueing were examined under conditions in which some stimuli appeared at locations that could not become the goal of a saccadic eye movement. It was observed that peripheral cues failed to elicit reflexive attentional orienting when targets appeared beyond the range of eye movements. Similarly, nonpredictive arrow cues were ineffective when targets could not become the goal of a saccade. In contrast, significant gaze-cueing effects were still observed when targets were beyond the range of eye movements. These data demonstrate that the mechanisms involved in gaze cueing are dissociated from those involved in exogenous orienting to peripheral or arrow cues. Furthermore, the findings suggest that, unlike peripheral cueing and reflexive arrow cueing, gaze cueing is independent of oculomotor control. We conclude that the premotor theory does not offer a compelling explanation for gaze cueing.

Keywords Gaze · Eye movement · Attention · Premotor theory · Arrow, Exogenous, Endogenous, Social

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Covert social attention refers to the automatic allocation of spatial attention in response to observing a social signal, such as a change in gaze direction. In the lab, social attention is often operationalized in gaze-cueing tasks (e.g., Friesen & Kingstone, 1998). In the canonical task, an observer fixates a centrally presented cue face that can look either left or right, and the observer must then respond to a stimulus that is congruent or incongruent with the gaze direction of the cue. Participants typically respond faster and more accurately when the stimulus is congruent with the gaze direction. Behaviorally, gaze cueing appears to be similar to the reflexive attentional orienting elicited by nonsocial stimuli, such as nonpredictive peripheral cues and nonpredictive arrow cues. Specifically, gaze cueing can occur very quickly (within 100 ms of stimulus onset) and is resistant to inhibition, such that attention is oriented in response to nonpredictive cues (Driver et al., 1999; Friesen & Kingstone, 1998; Friesen, Moore, & Kingstone, 2005). The phenomenon has attracted a great deal of research interest, but the neural mechanism underlying gaze cueing remains controversial.

One area of dispute concerns the role of the eye-movement system in gaze cueing. Several studies have shown that gaze cues elicit both covert attentional orienting and activation of saccade plans toward the gazed-at location (Hermens & Walker, 2010; Kuhn & Kingstone, 2009; Nummenmaa & Hietanen, 2006; Ricciardelli, Betta, Pruner, & Turatto, 2009; Ricciardelli, Bricolo, Aglioti, & Chelazzi, 2002), and recent neuroimaging data have indicated that observing shifts in gaze activates cortical areas involved in both attention and oculomotor preparation (Cazzato, Macaluso, Crostella, & Aglioti, 2012; Grosbras, Laird, & Paus, 2005). An appealing interpretation of these data is that gaze cues reflexively trigger motor preparation in the eye-movement system, and it is this oculomotor activation that biases attention to the gazed-at location. This account is consistent with the influential but controversial premotor theory of attention, which proposes that covert

attention is the consequence of activation in the oculomotor system (e.g., Rizzolatti, Riggio, & Sheliga, 1994), and with evidence that exogenous attention is mediated by the oculomotor system (Gabay, Henik, & Gradstein, 2010; Rafal, Posner, Friedman, Inhoff, & Bernstein, 1988; Smith, Ball, Ellison, & Schenk, 2010; Smith, Rorden, & Jackson, 2004; Smith, Rorden, & Schenk, 2012).

However, evidence of coactivation of motor plans and covert attention does not demonstrate that motor preparation *causes* the covert attention shift (Schneider, 1995; Smith & Schenk, 2012). Furthermore, not all studies have found an association between gaze cueing and oculomotor activity. For example, Friesen and Kingstone (2003) reported that gaze cueing does not interact with the gap effect (a facilitation of saccadic reaction times when the fixation point is removed prior to the onset of a saccadic target in the periphery). The gap effect is known to be mediated by activation of the superior colliculus (SC; Dorris & Munoz, 1995). Given that the SC is critically involved in the control of saccadic eye movements, Friesen and Kingstone (2003) argued that the failure to observe an interaction between gaze cueing and the gap effect is indirect evidence against a causal role for motor preparation in gaze cueing.

A more direct test of the role of saccade preparation in gaze cueing would be to measure gaze-cueing effects when preparation of saccadic eye movements is physiologically constrained. If gaze cueing depends on the preparation of a saccadic eye movement to the gazed-at location, the inability to plan a saccadic eye movement to that location should abolish the gaze-cueing effects. To test this prediction, we used a variant of the eye abduction paradigm developed by Craighero, Nascimben, and Fadiga (2004). In this task, participants are asked to abduct the eye by 40 deg, such that they fixate a point near the limit of their oculomotor range (see Fig. 1B). When the eye is in this position, probes in the temporal hemifield appear beyond the effective oculomotor

range (i.e., participants cannot plan a saccadic eye movement to fixate the probe positions; Guitton & Volle, 1987). This manipulation has been shown to disrupt attentional orienting to centrally presented spatially predictive cues (Craighero et al., 2004), to feature singletons but not conjunctions in visual search (Smith, Ball, & Ellison, 2014; Smith et al., 2010), and to peripheral but not symbolic cues (Smith et al., 2012). The manipulation also impairs rehearsal in spatial, but not visual, working memory (Ball, Pearson, & Smith, 2013).

If gaze cueing is contingent on the ability to plan a saccadic eye movement to the gazed-at location, then abduction of the eye should disrupt gaze cueing at locations that can no longer become the goal of a saccade. To test this prediction, the effect of eye abduction on gaze cueing was measured using a standard Posner-style cueing paradigm, and performance was compared across gaze-cueing, peripheral-cueing, and nonpredictive arrow-cueing tasks (note that the results of our nonpredictive arrow-cueing task would not be directly comparable to those of Craighero et al., 2004, because they used a predictive cue that probably engaged both endogenous and exogenous attentional mechanisms).

Method

Participants

A group of 22 participants volunteered for the experiment (15 female, seven male). Undergraduate participants enrolled on the Psychology or Applied Psychology degree programs received credit in the Department of Psychology participant pool for taking part. Other participants were paid £4. All participants gave informed consent before participating. The study was approved by the Department of Psychology Ethics Committee.

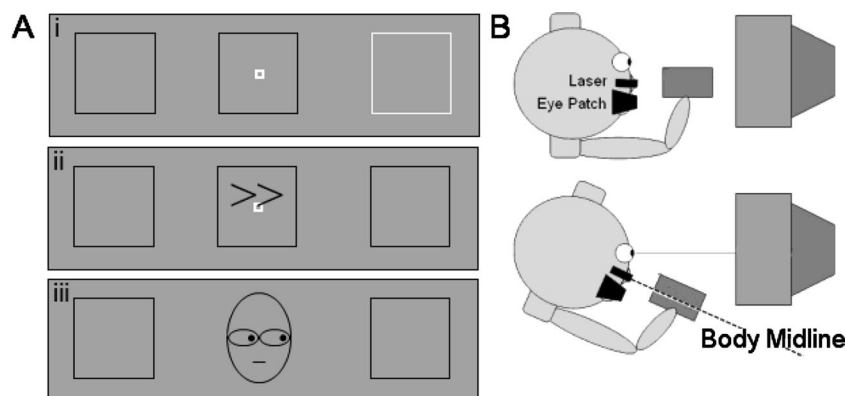


Fig. 1 Illustration of the experimental setup and procedure. Panel A shows examples of the three different cue types. Note that the (i) peripheral cues, (ii) arrow cues, and (iii) gaze cues were presented in different blocks of trials. Panel B shows the posture adopted in the eye-frontal and

eye-abducted conditions. The dotted line shows the midline of the head and body. In this case, the temporal hemifield is to the left of fixation, and the nasal hemifield is to the right of fixation

Apparatus

All stimuli were generated using a Cambridge Research Systems ViSaGe graphics card and displayed on a 100-Hz, 17-in. Sony Trinitron CRT monitor. Responses were collected using a button-box. A soft eye patch occluded the nonpreferred eye. A laser pointer was attached to the center of the forehead of the participant using a Velcro headband. A point corresponding to a 40-deg angle of abduction was marked on the wall. In the abducted condition, the participant fixated the center of the monitor and turned his or her body and head such that the laser beam intersected with this point (see Fig. 1B). If the participant moved the head to reduce the angle of abduction, the experimenter asked him or her to return to the correct position and marked the trial number so that it could be excluded from the analysis.

Eye movements were recorded using electrooculography via an MP35 acquisition unit and Acqknowledge software (Biopac Systems Inc., CA, USA). Only horizontal eye movements were measured: The two electrodes that measured the horizontal movements were placed adjacent to the temporal canthus of each eye, and the reference electrode was placed in the center of the forehead. The data were sampled at 500 Hz.

Stimuli

We created three cue types. The gaze cue was a black schematic face ($2.7^\circ \times 3.7^\circ$) filled with a gray background and presented such that the intersection of the eyes was at the exact center of the screen. Gaze cueing was achieved by positioning the black pupils (0.2°) such that the face appeared to be looking to the left or the right. The peripheral cue was a luminance change that occurred at one of two peripheral placeholders. The arrow cue consisted of two chevrons oriented left or right (i.e., “<<” or “>>”), subtending $1.8^\circ \times 0.5^\circ$, which were superimposed on the fixation point. The target was a small ($0.5^\circ \times 0.5^\circ$), light gray square. The center of the peripheral cues and targets appeared 6° away from fixation.

Procedure

The experiment was performed monocularly with the right eye, while the left eye was covered with a patch. Participants were positioned 57 cm away from the display with their heads in a chinrest. They were instructed to fixate the central fixation point and not to move their eyes during a trial. Blocks of trials contained only one type of cue. Each participant completed six blocks of 80 trials. Of these trials, 80 % of the trials were target-present, and 20 % were catch trials in which no target was presented. Two blocks of each cue type were presented, with participants completing one block in the frontal position

and one in the abducted position. The order of testing was counterbalanced across participants. Trials began with the onset of a fixation point flanked by two placeholders. This display was present for 1,000 ms, and then was replaced with the cue stimulus (gaze, peripheral luminance change, or arrow). The cue was present for 150 ms. The target appeared simultaneously with cue offset and remained visible until the participant made a response. Figure 1A illustrates the different cue types. Participants were instructed to press a button on the response box as quickly as possible when the target appeared. On catch trials, in which no target appeared, no response was required.

Results

One participant withdrew during testing. A second participant had reaction times (RTs) 3 *SDs* longer than the group mean reaction time and was excluded. Data were filtered to remove trials contaminated by eye movements ($n = 71$, <1 % of trials), anticipations with an RT of <150 ms (<0.1 % trials), and trials in which the RT was >2.5 *SDs* from an individual’s mean RT (3.8 % trials). The analyses for each type of cue are presented separately. In these analyses, hemifields were defined with respect to target position, to allow for direct comparisons to previous studies. It is possible to define hemifield with respect to cue position, but in this case validity would be confounded with hemifield.

Peripheral cueing

The mean RTs were subjected to a $2 \times 2 \times 2$ repeated measures analysis of variance (ANOVA) with the factors Eye Position, Hemifield, and Validity. The analysis revealed a main effect of validity [$F(1, 19) = 7.6, p < .05, \eta^2 = .29$] and a three-way interaction between eye position, hemifield, and validity [$F(1, 19) = 4.7, p < .05, \eta^2 = .20$]. Analysis of the effects of hemifield and validity when the eye was in the central position revealed a main effect of validity [$F(1, 19) = 10, p < .05, \eta^2 = .35$] but no interactions. In contrast, when the eye was in the abducted position, no main effects were found, but there was a significant interaction between hemifield and validity, such that RTs on valid trials were faster than those on invalid trials in the temporal hemifield (valid, 381 ms; invalid, 417 ms), but not in the nasal hemifield (valid, 404 ms; invalid, 408 ms). Figure 2 (left panels) illustrates these results.

Nonpredictive arrow cueing

The mean RTs were subjected to a $2 \times 2 \times 2$ repeated measures ANOVA with the factors Eye Position, Hemifield, and

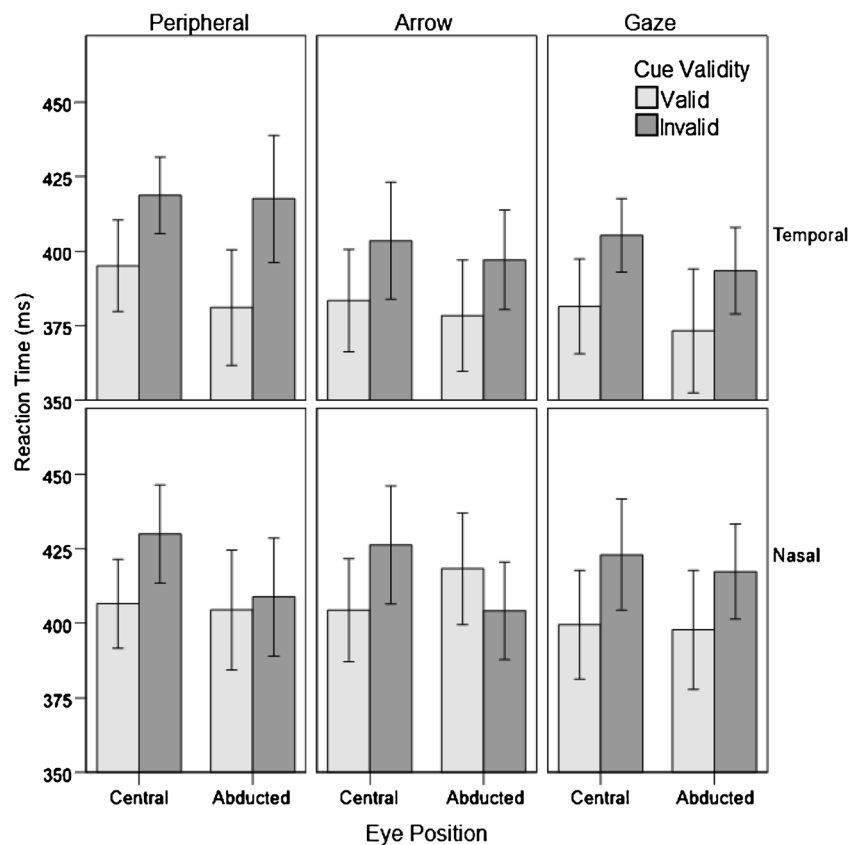


Fig. 2 Mean reaction times during valid and invalid cueing conditions in each eye position. We observed three-way interactions between eye position, hemifield of target, and validity for both peripheral and arrow cueing, but not for gaze cueing. Error bars show ± 1 SEM

Validity. The analysis revealed main effects of hemifield [$F(1, 19) = 15, p < .05, \eta^2 = .44$] and validity [$F(1, 19) = 7.5, p < .05, \eta^2 = .28$], a two-way interaction between eye position and validity [$F(1, 19) = 5.02, p < .05, \eta^2 = .21$], and a three-way interaction between eye position, hemifield, and validity [$F(1, 19) = 5.58, p < .05, \eta^2 = .23$]. Analysis of the effects of hemifield and validity when the eye was in the central position revealed a main effect of validity [$F(1, 19) = 14, p < .05, \eta^2 = .42$] but no interactions. In contrast, when the eye was in the abducted position, we found a main effect of hemifield [$F(1, 19) = 16.61, p < .05, \eta^2 = .45$] and a significant interaction between hemifield and validity [$F(1, 19) = 5.06, p < .05, \eta^2 = .21$], such that RTs on valid trials were faster than those on invalid trials in the temporal hemifield (valid, 378 ms; invalid, 396 ms), but not in the nasal hemifield (valid, 418 ms; invalid, 404 ms). The central panels of Fig. 2 illustrate these results.

Gaze cueing

The mean RTs were subjected to a $2 \times 2 \times 2$ repeated measures ANOVA with the factors Eye Position, Hemifield, and Validity. The analysis revealed main effects of hemifield [$F(1, 19) = 9.5, p < .05, \eta^2 = .33$] and validity [$F(1, 19) = 7.79, p < .05, \eta^2 = .29$] but, critically, no three-way interaction

between eye position, hemifield, and validity [$F(1, 19) = 0, p = .99, \eta^2 = .00$].

Figure 2 (right panels) illustrates these results.

Discussion

Our aim was to test the hypothesis that gaze-cueing effects are driven by the automatic activation of the eye-movement system in response to observing a change in gaze. In the present study, activation of the eye-movement system was restricted by presenting stimuli at locations at which they could be seen but could not be directly accessed by a saccadic eye movement. Several previous studies have demonstrated that this manipulation creates a deficit of exogenous attention that is specific to locations that are motorically inaccessible (Smith, Ball, & Ellison, 2014; Smith et al., 2010; Smith et al., 2012). Consistent with these findings, we observed that eye abduction disrupted peripheral cueing. Furthermore, we showed that exogenous orienting triggered by nonpredictive arrow cues was also disrupted by eye abduction. Critically, however, it was also shown that gaze cueing was intact at locations that could not become the goal of a saccade. This result is inconsistent with the proposal that gaze cueing is the consequence

of the automatic activation of oculomotor plans (e.g., Rizzolatti et al., 1994).

The finding that reflexive gaze-cueing effects are unimpaired by disruption to saccade planning is consistent with a previous study by Friesen and Kingstone (2003), who argued that the absence of an interaction between gaze cueing and the gap effect is evidence against the involvement of the superior colliculus in gaze cueing (see also Friesen et al., 2005). Together, these studies suggest that covert gaze cueing does not depend on covert motor preparation, and that the coactivation of the oculomotor system and gaze cueing observed in other studies (e.g., Hermens & Walker, 2010; Kuhn & Kingstone, 2009; Nummenmaa & Hietanen, 2006; Ricciardelli et al., 2009; Ricciardelli et al., 2002) should not be taken as evidence for a causal link between oculomotor activation and covert gaze cueing.

Proponents of a premotor explanation for gaze cueing might argue that although eye abduction disrupts the preparation of saccadic eye movements, participants could still have planned combined eye–head movements, and that the preparation of these movements mediated the endogenous attention shifts (e.g., Cicchini, Valsecchi, & de’Sperati, 2008). Although this account is theoretically plausible, no empirical evidence has indicated that preparing but not executing a head movement elicits a covert shift of attention. Indeed, evidence from studies of eye movements has indicated that preparing but not executing a saccade is not sufficient to elicit a covert shift of attention (Born, Mottet, & Kerzel, 2014; Hunt & Kingstone, 2003; Klein, 1980; Klein & Pontefract, 1994). Furthermore, exogenous attention is associated with activation of the head-movement system (Corneil, Munoz, Chapman, Admans, & Cushing, 2008), so it is not clear why the preparation of head movements should support endogenous orienting, but not exogenous orienting. Given these considerations, it seems unlikely that planned combined eye–head movements would mediate the gaze-cueing effect. However, the extent to which preparation of head movements is sufficient to elicit covert shifts of attention remains an empirical question.

The finding that eye abduction disrupted reflexive arrow cueing but not reflexive gaze cueing suggests that social attention and arrow cuing can be experimentally dissociated. This finding speaks to a long-standing debate regarding the extent to which arrow cueing and gaze cueing rely on similar neural substrates. According to one view, reflexive gaze cueing and arrow cueing both arise as a result of repeated exposure to associations between gaze/arrow direction and task-relevant stimuli, and are therefore the product of a common neural mechanism (e.g., Guzzon, Brignani, Miniussi, & Marzi, 2010; Trujillo & Schnyer, 2011). In contrast, others have argued that reflexive arrow cueing is mediated by the same neural systems as endogenous attention, whereas gaze cueing is mediated by distinct social–cognitive processes

(Nummenmaa & Calder, 2009). The issue has remained contentious partly because the neuroimaging data are conflicting. For example, some imaging studies have suggested that arrow cueing and gaze cueing have very similar psychophysiological correlates (Brignani, Guzzon, Marzi, & Miniussi, 2009; Chanon & Hopfinger, 2011; Guzzon et al., 2010), whereas others have argued that the neural correlates of arrows and gaze cueing are different (Hietanen, Leppänen, Nummenmaa, & Astikainen, 2008; Hietanen, Nummenmaa, Nyman, Parkkola, & Hämäläinen, 2006).

However, although the imaging data are open to conflicting interpretations, there is clear neuropsychological evidence for a double dissociation between gaze cueing and arrow cueing, such that lesions to superior temporal gyrus disrupt gaze cueing but not arrow cueing (Akiyama et al., 2006), whereas lesions to the frontal lobes impair arrow cueing but not gaze cueing (Vecera & Rizzo, 2006). Furthermore, two recent studies (Greene & Zaidel, 2012; Marotta, Lupiáñez, & Casagrande, 2012) have demonstrated a right hemisphere specialization for gaze cues that is not present for nonsocial cues, suggesting that they are mediated by different neural mechanisms. Although these results are not conclusive, the fact that eye abduction disrupted arrow cueing but not gaze cueing indicates that the different cue types are functionally different with respect to their relationship with the eye-movement system. This result is consistent with the neuropsychological evidence that arrow cueing and gaze cueing are mediated by different neural mechanisms.

To summarize, a number of studies have suggested that gaze cues activate the oculomotor system, leading to the proposal that covert, reflexive social orienting is the consequence of planned but unexecuted eye movements (the premotor theory of attention). However, these previous studies have typically reported associations between gaze cueing and oculomotor activation. Here, we showed that eye abduction disrupts reflexive orienting to peripheral cues and arrow cues, but not to gaze cues. This result clearly demonstrates independence between the ability to make a saccadic eye movement and reflexive social attention, demonstrating that the premotor theory does not apply to reflexive social attention.

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