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 the oculomotor activation is unclear. One extremely influential hypothesis is that 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 where 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, non-predictive arrow cues were ineffective when targets could not become the goal of a saccade. In contrast, significant gaze cueing effects were 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.

1. Introduction

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 operationalised in gaze cueing tasks (e.g. Friesen & Kingstone, 1998). In the canonical task an observer fixates a centrally presented cue face which can look left or right, and they must then respond to a stimulus that is congruent or incongruent with gaze direction of the cue. Participants typically respond faster and more accurately when the stimulus is congruent with gaze direction. Behaviourally, gaze cueing appears similar to reflexive attentional orienting elicited by non-social stimuli, such as non-predictive peripheral cues and non-predictive arrow cues. Specifically, gaze-cueing can occur very quickly (within 100ms of stimulus onset) and is resistant to inhibition, such that attention is oriented in response to non-predictive 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 towards 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 proposed that covert attention is the consequence of activation in the oculomotor system (e.g. Rizzolatti, Riggio, & Sheliga, 1994), and 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 co-activation 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) report 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 & Kingstone (2003) argue that the failure to observe an interaction between gaze-cuing 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 is 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 the gazed-at location should abolish gaze-cueing effects. To test this prediction we used a variant of the eye-abduction paradigm developed by Craighero and colleagues (Craighero, Nascimben, & Fadiga, 2004). In this task participants are asked to abduct the eye by 40 degrees, such that they fixate a point near the limit of their oculomotor range (see Figure 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), feature singletons but not conjunctions in visual search (Smith, Ball, & Ellison, 2014; Smith, et al., 2010) and 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 non-predictive arrow cueing tasks (note that the results of our non-predictive arrow cueing task will not be directly comparable to those of Craighero et al., 2004 because they used a predictive cue which probably engaged both endogenous and exogenous attentional mechanisms).

Method

1.1. Participants

Twenty-two participants volunteered for the experiment (7 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.

1.2.Apparatus

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

Eye-movements were recorded using EOG 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 centre of the forehead. Data were sampled at 500 Hz.

1.3.Stimuli

There were three cue types. The gaze-cue was a black schematic face (2.7° x 3.7°) filled with a grey background presented such that the intersection of the eyes was at the exact centre 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 right. The peripheral cue was a luminance change which occurred at one of two peripheral placeholders. The arrow cue consisted of 2 chevrons oriented left or right (i.e. “<<” or “>>”), subtending 1.8° x 0.5°, which were superimposed on the fixation point. The target was a small (0.5° x 0.5°), light grey square. The centre of the peripheral cues and targets appeared 6° away from fixation.

1.4.Procedure

The experiment was performed monocularly with the right eye. The left eye was covered with a patch. Participants were positioned 57cm away from the display with their head in a chinrest. They were instructed to fixate the central fixation point and not move their eyes during a trial. Blocks of trials contained only one type of cue. Each participant completed 6 blocks of 80 trials. 80% of trials were target present trials, 20% of trials were catch trials in which no target was presented. There were two blocks of each cue type and participants completed one block in the frontal position and one in the abducted position. 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 1000ms, and then was replaced with the cue stimulus (gaze, peripheral luminance change or arrow). The cue was present for 150ms. 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 fast as possible when the target appeared. On catch trials, where no target appeared, no response was required.

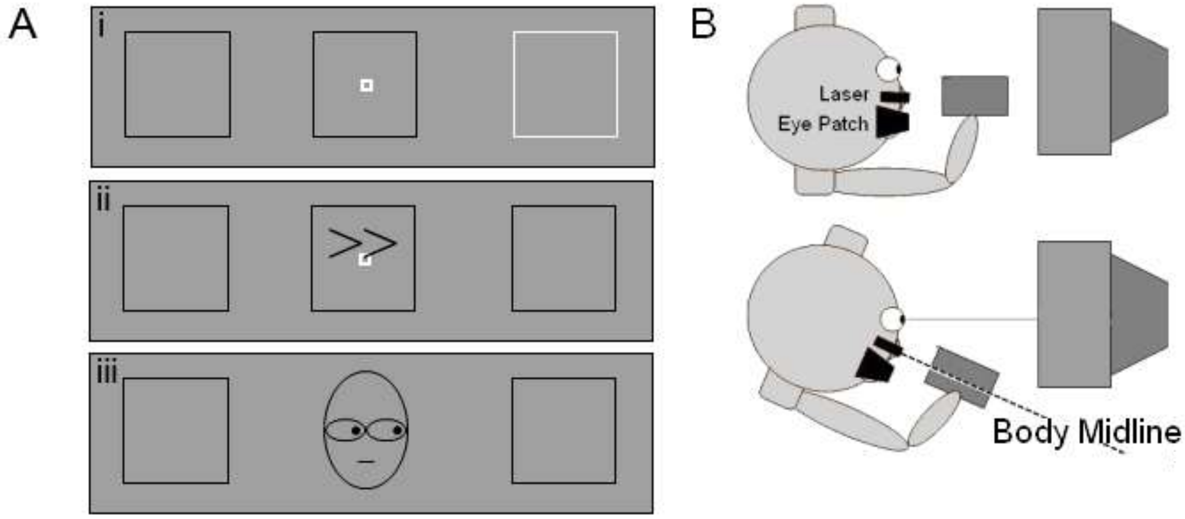

Figure 1: Illustration of the experimental setup and procedure. Panel A shows an example of the three different cue types. Note that peripheral cues (i) arrow cues (ii) and gaze cues (iii) were presented in different blocks of trials. Panel B shows the posture adopted in the eye frontal and eye-abducted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

2. Results

One participant withdrew during testing. A second participant had reaction times 3SD 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 <150ms (<0.1% trials) and trials where an RT was >2.5SD from an individual's mean RT (3.8% trials). The analyses for each type of cue are presented separately. In these analyses 'hemifield' was defined with respect to target position to allow for direct comparison to previous studies. It is possible to define hemifield with respect to cue position, but in this case Validity would be confounded with Hemifield.

2.1.Peripheral cueing.

Mean RTs were subjected to a 2x2x2 repeated measures ANOVA with factors of EyePosition, Hemifield and Validity. The analysis revealed a main effect of Validity ($F_{(1,19)} = 7.6$, $p < 0.05$, $\eta^2 = 0.29$) and a 3-way interaction between Eye Position, Hemifield and Validity ($F_{(1,19)} = 4.7$, $p < 0.05$, $\eta^2 = 0.20$). Analysis of the effects of Hemifield and Validity when the eye was in the Central position revealed a main effect of Validity ($F_{(1,19)} = 10$, $p < 0.05$, $\eta^2 = 0.35$) but no interactions. In contrast, when the eye was in the Abducted position there were no main effects, but there was a significant interaction between Hemifield and Validity, such that reaction times on Valid trials were faster than those on Invalid trials in the Temporal Hemifield (Valid: 381ms, Invalid 417ms) but not the Nasal hemifield (Valid: 404ms, Invalid 408ms). Figure 3 illustrates these results.

2.2.Non predictive arrow cueing

Mean RTs were subjected to a 2x2x2 repeated measures ANOVA with factors of Eye Position, Hemifield and Validity. The analysis revealed main effects of Hemifield ($F_{(1,19)} = 15$, $p < 0.05$, $\eta^2 = 0.44$) and Validity ($F_{(1,19)} = 7.5$, $p < 0.05$, $\eta^2 = 0.28$), a 2-way interaction between Eye Position and Validity ($F_{(1,19)} = 5.02$, $p < 0.05$, $\eta^2 = 0.21$) and a 3-way interaction between Eye Position, Hemifield and Validity ($F_{(1,19)} = 5.58$, $p < 0.05$, $\eta^2 = 0.23$). Analysis of the effects of Hemifield and Validity when the eye was in the Central position revealed a main effect of Validity ($F_{(1,19)} = 14$, $p < 0.05$, $\eta^2 = 0.42$) but no interactions. In contrast, when the eye was in the Abducted position there was a main effect of Hemifield ($F_{(1,19)} = 16.61$, $p < 0.05$, $\eta^2 = 0.45$) and a significant interaction between Hemifield and Validity ($F_{(1,19)} = 5.06$, $p < 0.05$, $\eta^2 = 0.21$), such that reaction times on Valid trials were faster than those on Invalid trials in the Temporal hemifield (Valid: 378ms, Invalid 396ms) but not the Nasal hemifield (Valid: 418ms, Invalid 404ms). Figure 3 illustrates these results.

2.3.Gaze cueing

Mean RTs were subjected to a 2x2x2 repeated measures ANOVA with factors of Eye Position, Hemifield and Validity. The analysis revealed main effects of Hemifield ($F_{(1,19)} = 9.5$, $p < 0.05$, $\eta^2 = 0.33$) and Validity ($F_{(1,19)} = 7.79$, $p < 0.05$, $\eta^2 = 0.29$) but, critically, no 3-way interaction between Eye Position, Hemifield and Validity ($F_{(1,19)} = 0$, $p = 0.99$, $\eta^2 = 0.00$). Figure 3c illustrates these results.

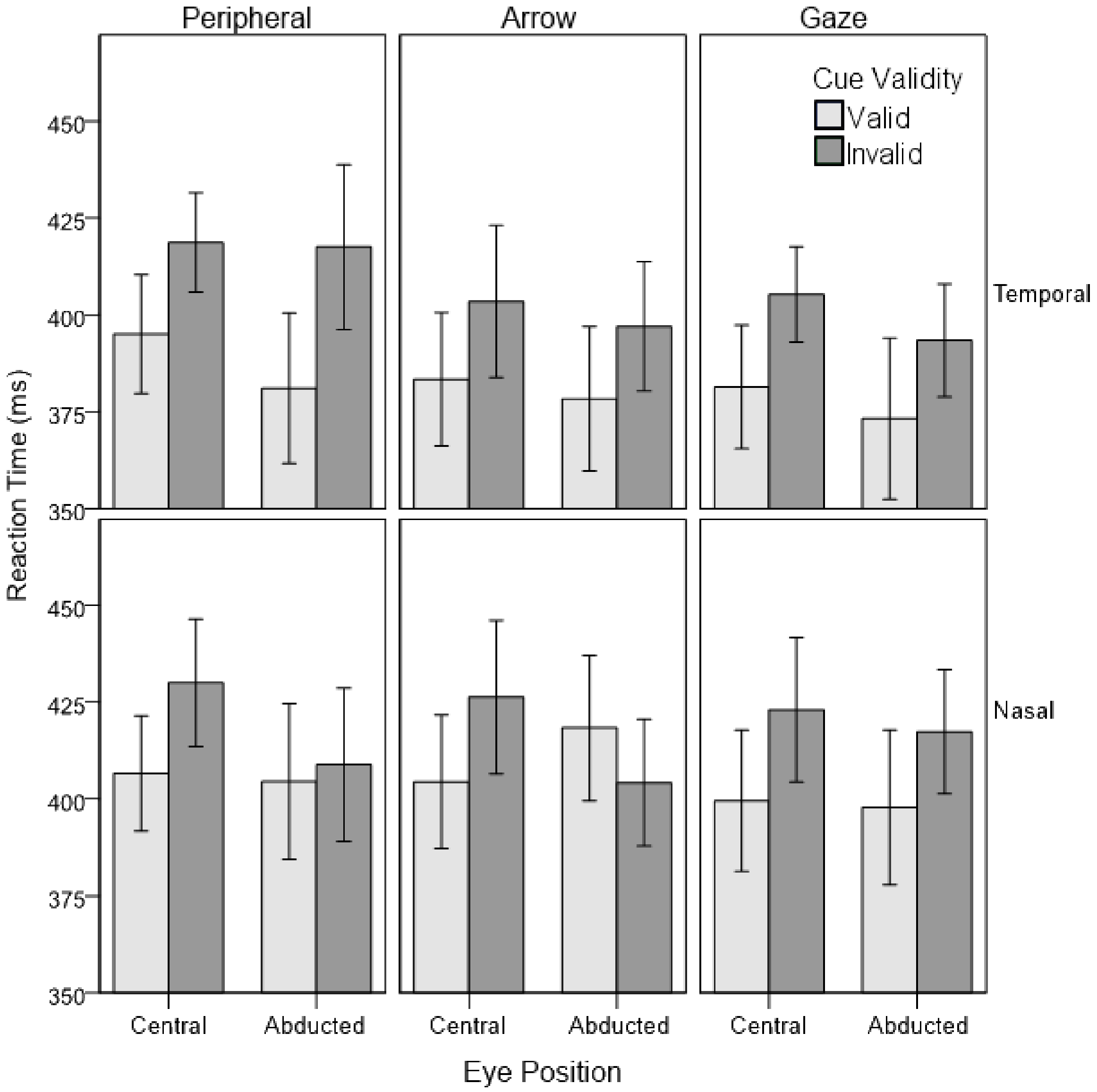

Figure 2. Mean reaction times during Valid and Invalid cueing conditions in each eye-position. There were 3-way interactions between Eye Position, Hemifield of Target and Validity for Peripheral Cueing and Arrow Cueing, but not Gaze Cueing. Error bars show +/-1 SEM.

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 current study, activation of the eye-movement system was restricted by presenting stimuli at locations where 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, it was shown that exogenous orienting triggered by non-predictive arrow cues is 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 & Kingstone (2003) who argue that an absence of an interaction between gaze cueing and the gap effect is evidence against the involvement of the superior colliculus in gaze cuing (see also Friesen, et al., 2005). Together, these studies suggest that covert gaze cueing does not depend on covert motor preparation, and that co-activation 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 it was the preparation of these movements that mediated the endogenous attention shifts (e.g. Cicchini, Valsecchi, & de'Sperati, 2008). While this account is theoretically plausible, there is no empirical evidence that preparing but not executing a head movement elicits a covert shift of attention. Indeed, evidence from studies of eye-movements indicates 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 are mediating 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. In 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 suggest 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 argue that the neural correlates of arrows and gaze cueing are different (Hietanen, Leppanen, Nummenmaa, & Astikainen, 2008; Hietanen, Nummenmaa, Nyman, Parkkola, & Hamalainen, 2006).

However, while 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 STG 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, Lupianez, & Casagrande, 2012) have demonstrated a right hemisphere specialisation for gaze cues which is not present for non-social cues, suggesting they are mediated by different neural mechanisms. Although 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 suggest 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 typically report associations between gaze cueing and oculomotor activation. Here it has been shown that eye-abduction disrupts reflexive orienting to peripheral cues and arrow cues but not 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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