

## Durham Research Online

---

### Deposited in DRO:

18 May 2012

### Version of attached file:

Accepted Version

### Peer-review status of attached file:

Peer-reviewed

### Citation for published item:

Smith, D.T. and Schenk, T. (2012) 'The Premotor theory of attention : time to move on?', *Neuropsychologia*, 50 (6). pp. 1104-1114.

### Further information on publisher's website:

<https://doi.org/10.1016/j.neuropsychologia.2012.01.025>

### Publisher's copyright statement:

NOTICE: this is the author's version of a work that was accepted for publication in *Neuropsychologia*. Changes resulting from the publishing process, such as peer review, editing, corrections, structural formatting, and other quality control mechanisms may not be reflected in this document. Changes may have been made to this work since it was submitted for publication. A definitive version was subsequently published in *Neuropsychologia*, 50, 6, May 2012, 10.1016/j.neuropsychologia.2012.01.025

### Additional information:

## Use policy

---

The full-text may be used and/or reproduced, and given to third parties in any format or medium, without prior permission or charge, for personal research or study, educational, or not-for-profit purposes provided that:

- a full bibliographic reference is made to the original source
- a [link](#) is made to the metadata record in DRO
- the full-text is not changed in any way

The full-text must not be sold in any format or medium without the formal permission of the copyright holders.

Please consult the [full DRO policy](#) for further details.

# The Premotor Theory of Attention: Time to Move on?

Daniel T. Smith<sup>1\*</sup> and Thomas Schenk<sup>2</sup>

<sup>1</sup> Department of Psychology, Durham University, Queens Campus, Stockton on Tees, TS176BH, UK

<sup>2</sup> Department of Neurology, University of Erlangen-Nuremberg, 91054 Erlangen, Germany

Keywords: Attention, Ophthalmoplegia, Inhibition of Return, Eye-abduction, Premotor, Capture, Cueing, Peripheral, Nasal, Temporal, Oculomotor, IOR, Symbolic, Voluntary, Reflexive

\*Correspondence to: [daniel.smith2@durham.ac.uk](mailto:daniel.smith2@durham.ac.uk); Phone: 0191 3340474

## **Abstract**

Spatial attention and eye-movements are tightly coupled, but the precise nature of this coupling is controversial. The influential but controversial Premotor theory of attention makes four specific predictions about the relationship between motor preparation and spatial attention. Firstly, spatial attention and motor preparation use the same neural substrates. Secondly, spatial attention is functionally equivalent to planning goal directed actions such as eye-movements (i.e. planning an action is both necessary and sufficient for a shift of spatial attention). Thirdly, planning a goal directed action with any effector system is sufficient to trigger a shift of spatial attention. Fourthly, the eye-movement system has a privileged role in orienting visual spatial attention. This article reviews empirical studies that have tested these predictions. Contrary to predictions one and two there is evidence of anatomical and functional dissociations between endogenous spatial attention and motor preparation. However, there is compelling evidence that exogenous attention is reliant on activation of the oculomotor system. With respect to the third prediction, there is correlational evidence that spatial attention is directed to the endpoint of goal-directed actions but no direct evidence that this attention shift is dependent on motor preparation. The few studies to have directly tested the fourth prediction have produced conflicting results, so the extent to which the oculomotor system has a privileged role in spatial attention remains unclear. Overall, the evidence is not consistent with the view that spatial attention is functionally equivalent to motor preparation so the Premotor theory should be rejected, although a limited version of the Premotor theory in which only exogenous attention is dependent on motor preparation may still be tenable. A plausible alternative account is that activity in the motor system contributes to biased competition between different sensory representations with the winner of the competition becoming the attended item.

## **Introduction**

Attention allows observers to select behaviourally relevant sensory inputs for further processing while simultaneously suppressing the processing of irrelevant stimuli. The focus of attention can be oriented reflexively in response to salient events in the environment (exogenous attention), or voluntarily, in response to the goals and desires of the observer (endogenous attention). According to information processing models of attention information enters the sensory or motor system and is then relayed into memory via an attentional mechanism that is independent of the sensory and motor system. In other words, attention is conceived as a modular, 'higher' cognitive function, akin to language or memory. These models of attention have been very successful in accounting for behavioural data. However, they have faced problems trying to relate theoretical accounts of attention to the neurobiology of the visual system. More specifically, it has proved difficult to identify specific neural substrates of spatial attention which are a necessary precondition for any modular model of cognitive function.

One influential but controversial idea that can explain why it has been difficult to localise the neural substrates of attention is that spatial attention is actually generated in the neural systems used to plan and execute actions. In other words, it has been difficult to discover specific neural substrates of spatial attention because no such substrates exist. One specific version of this idea, the Oculo Motor Readiness Hypothesis (OMHR), was proposed and rejected by Klein (1980) on the basis of data that seemed to show that preparing an eye-movement did not facilitate perception, and that paying attention did not speed-up saccadic reaction times. However, Rizzolatti et

al., (1987) rejected Klein's interpretation of the data and reformulated the OMHR as the Premotor theory of attention (Rizzolatti, Riggio, Dascola, & Umiltà, 1987). Their arguments and counterarguments are discussed more fully in section 4.

According to the Premotor theory of attention, spatial attention is the consequence of activation of the motor system, and that shifts of attention are achieved by planning goal-directed actions such as reaches and eye-movements. More specifically, the Premotor theory has four tenets that set out the hypothetical role of the motor system in controlling spatial attention. Firstly, spatial attention is a consequence of activating neurons located in the spatial maps used to plan movements. In other words, selective attention and movement planning use the same neural substrates and there is no independent attention system. Secondly, activation of these neurons depends on the preparation to perform goal-directed spatially coded movements (i.e. spatial attention is the consequence of planning goal-directed actions). Thirdly, different spatial pragmatic maps become active according to the task requirements. Spatial attention can therefore potentially originate from any effector system that can perform a goal-directed action. Finally although action preparation in any effector system can orient attention, the oculomotor system has a privileged role in selective spatial attention (Rizzolatti, Riggio, & Sheliga, 1994).

The Premotor theory has been particularly influential as its tenets give rise to four clear, testable predictions about the relationship between attention and motor control. Firstly, attention and motor control should use identical neural substrates. Secondly, covert spatial attention is functionally equivalent to motor preparation, such that action preparation is both necessary and sufficient for orienting of spatial attention. Thirdly, motor preparation with any effector system should be sufficient to

produce a shift of attention. Finally, if there is competition between motor plans in different effector systems, attention should be preferentially directed to the endpoint of eye-movements.

The predictions of the Premotor theory are controversial. In particular, the idea that covert motor preparation is both necessary *and* sufficient for spatial attention has been hotly debated. The goal of this review is to provide an overview of the evidence for and against the different predictions of the Premotor theory, draw a conclusion about the validity of the theory and identify the aspects of the theory which require revision and further characterization.

## **2. Attention and motor control use the same neural circuits**

The Premotor theory predicts that attention and motor control should utilise the same neural circuits. This prediction has been extensively investigated with respect to the eye-movement system. On first inspection there appears to be very compelling evidence for an overlap between the motor and attention systems in humans. Firstly, neuroimaging studies in humans show that preparing to move the eyes to a location activates the same network of frontal and parietal cortical regions as covertly attending (Beauchamp, Petit, Ellmore, Ingeholm, & Haxby, 2001; Corbetta et al., 1998; de Haan, Moryan, & Rorden, 2008; Nobre, Gitelman, Dias, & Mesulam, 2000; Perry & Zeki, 2000). [Figure 1, taken from de Haan et al., \(2008\) illustrates the extent of the overlap observed using neuroimaging.](#) Secondly, Transcranial Magnetic Stimulation (TMS) of the frontal component of the oculomotor system, specifically

the Frontal Eye Field (FEF) disrupts saccadic preparation (Beckers, Canavan, Zangemeister, & Homberg, 1992; Muri, Hess, & Meienberg, 1991; Muri, Vermersch, Rivaud, Gaymard, & PierrotDeseilligny, 1996; Thickbroom, Stell, & Mastaglia, 1996; Zangemeister, Canavan, & Hoemberg, 1995), modulates spatial attention during arrow cueing (Grosbras & Paus, 2002; Smith, Jackson, & Rorden, 2005; Smith, Jackson, & Rorden, 2009) and conjunction visual search tasks (Muggleton, Juan, Cowey, & Walsh, 2003), and modulates the sensitivity of extrastriate cortex in a manner analogous to endogenous attention (Ruff et al., 2008; Ruff et al., 2006; Silvanto, Lavie, & Walsh, 2006; Taylor, Nobre, & Rushworth, 2007). Similarly, TMS over posterior areas (i.e. Posterior Parietal Cortex, PPC) delays saccades (Beckers et al., 1992; Muri et al., 1996; Zangemeister et al., 1995) and conjunction search (Ellison, Rushworth, & Walsh, 2003; Sack et al., 2002) but, somewhat surprisingly, does not affect feature search (Ellison et al., 2003; Muggleton et al., 2008) unless the participant is required to execute an action to the target (Lane, Smith, Schenk, & Ellison, 2011).

\*\*\*FIGURE 1 HERE?\*\*\*

Thirdly, electrical microstimulation of FEF neurons can elicit fixed-vector saccadic eye-movements (i.e. the FEF neurons always produces a saccade of the same amplitude and direction) and shifts in spatial attention. Moore and colleagues mapped the location of one of these motor fields in monkeys, then repeated the stimulation but this time using an intensity that was lower than that required to actually elicit an eye-movement. The monkeys produced significantly enhanced perceptual discrimination when probes were presented in the motor fields of stimulated neurons, even though the monkey was still centrally fixated (Moore, Armstrong, & Fallah, 2003; Moore &

Fallah, 2001). Furthermore, the same subthreshold microstimulation protocol modulates the sensitivity of neurons in V4 whose visual receptive fields overlap the motor field (Armstrong, Fitzgerald, & Moore, 2006; Moore & Armstrong, 2003) in a way that is analogous to the modulation observed when the monkey endogenously attends to the location (Armstrong et al., 2006).

These data are often interpreted as evidence of functional equivalence between saccade preparation and covert attention. However, this interpretation of data from the FEF is problematic for the following reason; FEF contains multiple overlapping *but independent* neuronal populations, some of which are involved in visual selection but not motor control, and others that are involved in saccade control but not visual attention (Sato & Schall, 2003; Thompson, Bichot, & Schall, 1997; Thompson, Biscoe, & Sato, 2005). In other words, contrary to the predictions of the Premotor theory, the FEF neurons that drive saccadic eye-movements are separate from the neurons that drive visual selection. Microstimulation activates all neural tissue surrounding the electrode tip (Tehovnik, 1996) and so it is not possible to know whether the modulation of V4 is driven by visual or motor signals. It is for this reason that microstimulation does not provide unambiguous support for the Premotor theory. TMS activates even larger neuronal populations than microstimulation, so studies showing that TMS over FEF modulates spatial attention (Grosbras & Paus, 2002; Muggleton et al., 2003; O'Shea, Muggleton, Cowey, & Walsh, 2004; Silvanto et al., 2006; Smith et al., 2005) cannot be used as evidence in favour of the Premotor theory as it is not clear that the attentional modulation is being driven by specific activation of the motor system.

There are also reasons to be cautious in interpreting the observation of both delayed saccades and disrupted covert attention following parietal TMS as evidence for the premotor theory. Firstly, although regions in the Intraparietal Sulcus (IPS) appear to be activated during both saccadic preparation and covert attention (Andersen, Snyder, Batista, Buneo, & Cohen, 1998; Colby, Duhamel, & Goldberg, 1996; Gaymard, Ploner, Rivaud, Vermersch, & Pierrot-Deseilligny, 1998) it is important to note that this activation does not predict saccade onset or the locus of attention (Bisley & Goldberg 2003). Rather, it seems that activity in IPS represents a priority map which signals the location of behaviourally relevant stimuli. This signal can be used to select the location for further processing (i.e. to determine the locus of attention), or to guide saccadic eye-movements (Bisley & Goldberg 2003; Bisley & Goldberg 2010; Fecteau and Munoz 2006). Critically, this priority map emerges via the interaction of top-down intentions and bottom-up signals coding the salience of external stimuli, and is not determined solely by the intention to make an eye-movement. Thus, the existence overlapping activations during saccades and attention in IPS does not demonstrate that motor preparation and covert attention are functionally equivalent. Secondly, other areas implicated in visuospatial attention during visual search are localised in the inferior parietal lobule (Chambers, Payne, & Mattingley, 2007; Chambers, Payne, Stokes, & Mattingley, 2004; Chambers, Stokes & Mattingley 2004) or superior temporal sulcus (Ellison, Schindler, Pattison, & Milner, 2004; Schindler, Ellison, & Milner, 2008). However, these brain areas do not appear to have a clearly defined role in motor preparation. These data suggest that, as with FEF, saccade control and spatial attention are spatially segregated in PPC.

To summarize, functional brain imaging suggests that covert attention and oculomotor control use the same frontal and parietal regions, but a finer-grained

analysis using TMS in humans and single cell recording in non-human primates shows that within these structures there are separate neural networks for controlling saccades and covert attention. In other words, not all areas involved in motor preparation are involved in covert attention, and not all regions involved in covert attention have motor functions. These results are contrary to the predictions made by the Premotor theory, which holds that covert attention is the result of activation of the neural networks involved in action preparation. Thus, the first prediction of the Premotor theory is not strongly supported by existing empirical evidence.

### **3. Motor activation is sufficient for spatial attention**

The Premotor theory argues that motor preparation is functionally equivalent to a shift of attention, such that the locus of attention is directed to the goal of an incipient movement. This link between movement goal and locus of attention is mandatory, in the sense that preparing an action always results in the endpoint of the action being attended. If this hypothesis is correct, then the locus of spatial attention should always correspond to the endpoint of upcoming movements, even before the movement has been executed. Early attempts to test this prediction found reliable attentional enhancement at the endpoint of upcoming eye-movements, even when the probe was equally likely to appear at the location opposite the saccade endpoint (Shepherd, Findlay, & Hockey, 1986). However, in this task the stimuli remained present until participants responded, so it's possible that on some trials participants were able to fixate the probe, making it difficult to tease apart the effects of attention

from the effects of foveating the probe. This methodological issue was addressed by Hoffman & Subramaniam (1995). In Experiment 1, they observed attentional facilitation at the saccade goal when participants were required to discriminate the shape of a probe that disappeared prior to saccade onset. Furthermore, in Experiment 2 they explicitly instructed participants to attend to the location opposite the saccade goal, and still observed attentional facilitation at the saccade goal. Using a slightly different methodology Deubel & Schneider (1996) found that attention was locked to the saccade goal during a delayed-saccade task, to the extent that performance was poorer when attentional probes were presented as little as 1.5 degrees of visual angle away from the saccade goal. These presaccadic shifts of attention can also be observed prior to involuntary saccades to a distractor (Peterson, Kramer, & Irwin, 2004) and can elicit crossmodal shifts of auditory (Rorden & Driver, 1999) and tactile attention (Rorden, Greene, Sasine, & Baylis, 2002), although these crossmodal attention shifts are not as tightly coupled to the saccade goal as unimodal visual attention. For example, when Rorden et al., (2002) changed their paradigm so that participants expected the tactile stimulation to occur contralaterally to the saccade goal, the presaccadic attention shift was abolished. These data are typically taken as evidence that saccade preparation is sufficient to orient spatial attention, as predicted by the Premotor theory.

However, it is necessary to be cautious in interpreting the results of these studies as evidence of a complete, mandatory coupling between the goal of an upcoming movement and the locus of attention as there is evidence that top-down cognitive processes can influence the locus of attention. For example Kowler and colleagues (Kowler, Anderson, Doshier, & Blaser, 1995) observed that it was possible to endogenously attend to stimulus locations other than the saccade endpoint without

disrupting the metrics of the eye-movement. Specifically, they observed a strict coupling between the saccade goal and the locus of attention when participants prioritized the speed of their eye-movements. Conversely, when participants prioritized the attentional task, eye-movements were delayed (suggesting that oculomotor resources were required for the perceptual task). However, when asked to balance the eye-movement and perceptual task, participants could benefit from *some* attentional facilitation at the location of the perceptual task without disrupting the latency or accuracy of the eye-movement (although the attentional facilitation was significantly less than that observed when participants prioritized the perceptual task). Similarly, Montagini and Castet (2007) showed that participants can endogenously orient attention away from a saccade goal, but that this ability varied over time, such that progressively more attention was allocated to the saccade goal as movement onset approached.

One way to account for this apparent ability to attend to locations other than the saccade goal within the confines of the Premotor theory is to propose that both the attentional probe and saccade goal are encoded as the endpoints of a double-step saccade that first fixates the saccadic target, then the probe location. Consistent with this account, Godijn and Theeuwes (2003) have shown that during a double-step saccade task attention is allocated to the endpoints of both eye-movements in parallel. Similarly, Baldauf and Deubel (2008a) report attentional facilitation at the endpoint of up to three saccades and no facilitation at locations that are irrelevant for the saccade task, even when they lie on the path between two successive fixations. Attentional facilitation can be also observed at multiple saccade goals even when a saccade to only one of the goals is actually executed (Van der Stigchel & Theeuwes, 2005). Thus, the finding of attentional facilitation at behaviourally relevant locations that are

not the goal of the upcoming saccade can be accommodated within the Premotor theory of attention, so long as one assumes that the observer is planning an eye-movement of more than one step.

A second issue to consider with respect to the relationship between saccade preparation and covert attention is the time-course of the coupling. Given that the strength of oculomotor activity increases over time until saccade onset, and attention is associated with the strength of premotor activity, Premotor theory would predict that strength of the attentional allocation to the saccade goal should co-vary with the strength of oculomotor activation. To investigate this issue, Dore-Mazars, Pouget & Beauvillain (2004) attempted to more precisely characterise the time-course of pre-saccadic shifts of attention. Consistent with the Premotor theory, they observed a gradual build up of attention at the saccade goal, until attention was fully allocated at the saccade goal 50 milliseconds (ms) prior to saccade onset. Similarly, several other studies have reported that although it is possible to endogenously orient attention away from the saccade goal, the capacity to dissociate saccade goal and locus of attention decreases as the onset of the saccade gets closer (Deubel, 2008). However, if the saccade is signalled then delayed, attention remains locked to the saccade goal even during delays of up to 1300 ms before the onset of the eye-movement (Deubel & Schneider, 2003), suggesting that once the saccade is fully programmed and ready to execute, it's impossible to orient attention away from the saccade goal.

The Premotor theory predicts that action preparation in any effector system will be sufficient to elicit a shift of attention. Initial attempts to test this idea used a methodology similar to that employed in studies of the oculomotor system, such that participants would prepare a manual action and simultaneously make a perceptual

judgement about a stimulus that was congruent or incongruent with the direction of the action. Contrary to the predictions of the Premotor theory, Fischer (1997) observed no attentional facilitation when the perceptual target was congruent with the direction of pointing. However, in Fischer's task the perceptual target was in the same hemisphere as the planned action, but was not presented at movement endpoint. A subsequent study by Deubel, Schneider & Paprotta (1998) required participants to point to one of six targets, any of which could also contain a discrimination target which was presented for 120 ms and extinguished before movement onset. These targets were separated by only 1.5 degrees of visual angle, yet participants performed significantly better when the target was congruent with the movement endpoint. Indeed, the spatial specificity of attention shifts that precede actions is such that when a grasp is planned rather than a pointing action, attention is allocated only to the points of the object which will be in contact with the effector, and not the whole object (Schiegg, Deubel, & Schneider, 2003). Furthermore, facilitation at movement goals can be observed for both unimanual and bimanual pointing movements (Baldauf & Deubel, 2008b). Converging neurophysiological evidence that attention is allocated to the end point of pointing movements has been provided by Eimer, Forster, Van Velzen, and Prabhu (2005). They demonstrated that ERPS generated by irrelevant visual probes near the goal of a movement are enhanced relative to those generated by probes at other locations, consistent with the idea that visual attention has shifted to the movement goal.

Shifts of attention which precede manual actions share a number of behavioural features with pre-saccadic attention shifts. Schneider and Deubel (2002) demonstrated that peripheral visual cues that are presented within 120 ms of movement onset only capture attention if they appear at the movement endpoint,

suggesting that attention is locked to the location that has been selected in the motor system. More recently, Gherri and Eimer (2010) demonstrated that planning a manual action to one location severely disrupted the ability to attend to other locations, suggesting that once a location is selected in the motor system covert attention is locked to this location. Furthermore, as with presaccadic attention, attention appears to be directed to all pointing goals in a sequence of movements in parallel (Baldauf & Deubel, 2009; Baldauf, Wolf, & Deubel, 2006). However, pre-pointing attention shifts are only observed when the hand is visible. If vision of the arm is occluded, no attentional facilitation is observed, even when targets are presented close to the felt end-point of the hand (Bonfiglioli, Duncan, Rorden, & Kennett, 2002).

The Premotor theory proposes that spatial attention arises out of the activation of spatial maps that are specific to effector systems. If this is correct, simultaneously planning actions to different locations with different effectors should give rise to separate foci of attention (one at each movement endpoint). Jonikaitis & Deubel (2011) have recently tested this prediction using a discrimination task to measure attention. Consistent with the Premotor theory, they observed that simultaneously planning and executing arm and eye-movements to different locations produced attentional benefits at both movement goals. Furthermore, when saccades and reaches were directed to the same goal, the attentional enhancement was greater than when only a saccade or only a reach was planned. These data are consistent with the idea that motor preparation in different effector systems produces independent shifts of attention. However, contrary to these findings, Khan, Song & McPeck (2011) found that simultaneous saccades and manual pointing to different locations produced a single locus of attention at saccade goal, and there was no additive effect when saccade and reach were directed to the same goal. Furthermore, performance at the

reach goal during combined trials where a saccade and a reach were directed at different goals was poorer than performance in the reach only condition. They suggest that reach preparation and saccade preparation draw on a shared supramodal attentional rather than an effector-specific attentional resource.

The evidence for a mandatory link between action preparation and covert attention is compelling and consistent with the Premotor theory, in so far as motor preparation is sufficient to orient covert attention. However, Duhamel, Colby & Goldberg (1992) have suggested a physiologically plausible mechanism which can account for the coupling between oculomotor activity and attentional shifts but which does not require the assumption that attention shifts are dependent on motor preparation in covert-attention paradigms where subjects are instructed to refrain from making eye-movements to the location of upcoming visual targets.

More specifically, Duhamel Colby and Goldberg (1992) observed that in the moments before an eye-movement the visual system undergoes a radical remapping process that changes the response properties of visually responsive neurons in Lateral Intraparietal Sulcus (LIP), FEF and extrastriate cortex (Duhamel, Colby, & Goldberg, 1992; Nakamura & Colby, 2002). The consequence of this remapping is that some neurons begin to respond to stimuli at their anticipated post-saccadic location before the saccade has been executed. In the case of stimuli at the saccade goal, this means receptors that normally respond to foveal stimulation start responding to stimulation at the saccade endpoint. As there are relatively more of these receptors the relative signal-to-noise ratio of the stimulus at the saccade endpoint is greatly enhanced and it becomes 'attended' in the sense that information from the intended saccade goal is processed faster and more efficiently. Critically, this remapping does not occur prior

to endogenous shifts of attention where no movement is executed (Bushnell, Goldberg, & Robinson, 1981; Wurtz & Mohler, 1976), suggesting that pre-saccadic attentional shifts and shifts of covert attention (i.e. attention shifts in the absence of saccadic movements) are produced by different physiological mechanisms. Consistent with the idea that presaccadic attention is qualitatively different from endogenous spatial attention, presaccadic enhancement of visual perception can be dissociated from endogenous attentional enhancement of perception in a patient with optic ataxia (Khan et al., 2009)

Furthermore, the apparently mandatory link between attention and action can be accounted for in alternative selection-for-action frameworks (e.g. Schneider 1995; Schneider & Deubel 2002). These models argue that planning a goal directed action first requires a shift of attention to the goal location in order to encode its spatial position. In other words, Selection for Action (SfA) proposes a mandatory coupling between action preparation and spatial attention, but argues that this coupling arises because action preparation is impossible without first attending to the goal of the action. Thus SfA assumes that attentional shifts to the location of the action goal are a precondition of action preparation not just its by-product as assumed by the Premotor theory. The SfA account thus posits a separate mechanism for the spatial control of attention which will be recruited by upcoming actions but can also operate in the absence of movement preparation. A critical difference between SfA models and Premotor theory is that SfA proposes that covert attention is a necessary precondition for goal-directed movement preparation, but makes no assumptions about the involvement of the motor system in covert attention when goal directed actions are not required. In contrast, the Premotor theory proposes that motor preparation is a necessary precondition for covert attention, irrespective of whether or not an action is

to be executed. In a nutshell both accounts predict that motor preparation is a sufficient condition for attentional shift, but only the Premotor theory predicts that motor preparation is also necessary condition for attentional shift. We will evaluate this specific prediction in the next section.

To summarize, there is compelling evidence that overt, goal-directed eye and arm movements are preceded by a shift of attention. Superficially these data appear to confirm the prediction of the Premotor theory that motor preparation is sufficient for spatial attention. However, the data are equally well explained by SfA models which propose the exact opposite of Premotor theory (i.e. that covert attention is a necessary precondition for motor preparation), and there is converging evidence that the attention shifts that precede eye-movements are qualitatively different from endogenous attention shifts that are generated when the eyes remain stationary. The empirical data therefore provide evidence that motor preparation is sufficient for spatial attention; whether it is also necessary for spatial attention will be discussed in the next section.

#### **4. Motor preparation is necessary for spatial attention**

Spatial attention can be deployed covertly, such that the locus of attention is independent of the current direction of gaze (Posner, 1980). These covert attention shifts can be triggered endogenously in response to the goals and desires of the observer (e.g. looking both ways before crossing the street) or reflexively in response to salient events in the environment (e.g. responding to an unexpected car horn)

(Jonides, 1981; Posner & Cohen, 1984). In the lab, endogenous attention is typically manipulated using symbolic cues (e.g. an arrow cue or other instruction) that indicate the probable location of a target stimulus, or search tasks that require systematic exploration of an array of items. Exogenous attention is typically manipulated using salient peripheral cues that do not predict target location, or search tasks where one of the items is of relatively higher salience than the other items in the array. There are many dissociations between the time-course and behavioural consequences of exogenous and endogenous attention shifts (see Klein, 2009 for a recent review). For example, endogenous attention is relatively slow to deploy, and requires conscious cognitive effort but creates a sustained enhancement at the attended location (e.g. Muller & Rabbitt, 1989). In contrast, reflexive attention shifts are rapid and automatic but short-lived and superseded by a sustained inhibitory effect at the location of the salient event, known as Inhibition of Return (Posner, Rafal, Choate, & Vaughan, 1985). These dissociations have led many theorists to propose that exogenous and endogenous attention are mediated by independent cognitive mechanisms.

On first inspection the fact that attention can be oriented independently of an eye-movement would appear problematical for the Premotor theory, which argues that attention depends on neural activity related to movement. However, the claim of the Premotor theory is that motor preparation is required for attention, not motor execution. In the case of covert endogenous attention, Premotor theory argues that the observer plans a movement (usually an eye-movement), but withholds its execution.

The idea that oculomotor preparation is required for endogenous spatial attention was actually proposed and rejected by Klein seven years before the publication of the Premotor theory. In a classic paper Klein (1980) investigated

interactions between covert endogenous attention and oculomotor preparation using a dual task. In one version of the task participants were instructed to plan a saccade to the left or right. On 70% of trials they were then given a go signal to execute that movement, on 10% of trials they were given a signal to execute a saccade in the direction opposite to that which had been prepared and on 20% of trials the go signal was withheld and instead a visual probe was presented to which the participant should react as fast as possible. The probe could appear at the saccade goal or at the contralateral location. In the second version of the task participants were instructed to attend left or right. On 70% of trials a visual target was then presented at attended location, on 10% of trials it was presented at the unattended location, but on 20% of trials no target was presented and the participants were instead instructed to make a saccade to the attended or unattended location. Klein argued that if saccade preparation is necessary to orient covert attention (a) responses should be faster at the goal of the planned saccade than the contralateral location and (b) saccades to attended locations should have shorter latencies than saccades to unattended locations. Contrary to these predictions, when the primary task was to make a saccade, no attentional facilitation was observed when the probe overlapped with the saccade goal. Furthermore, when the primary task was to attend, no facilitation of saccadic response time was observed for saccades toward the attended location. Klein concluded that these results demonstrate independence of the oculomotor system and endogenous attention system.

The proponents of the Premotor theory objected that as there was no objective measure of saccade preparation in this study it was impossible to rule out the possibility that participants simply waited until the go signal was presented before planning their movements (Rizzolatti et al., 1987). Klein & Pontefract (1994)

attempted to address this issue by replicating the experiment and simultaneously monitoring saccadic performance. Consistent with previous results, no perceptual facilitation was observed at the goal of planned but unexecuted saccades and no facilitation was observed for saccades towards attended locations. Furthermore, saccades were significantly faster when the verbal instruction for saccade preparation matched the eventual direction of saccade execution compared to trials where there was a mismatch. Klein & Pontefract argue that this result demonstrates that participants were preparing an eye-movement in response to the verbal cue, and that saccade preparation is neither necessary nor sufficient for covert attention. However, this interpretation is problematic for two reasons. Firstly, even though saccadic latencies were shorter when the direction of movement specified at the planning and execution stages were congruent compared to when they were incongruent (341ms vs 422ms), the saccadic latencies were still relatively long, suggesting that participants were not simply releasing a pre-programmed saccade, but actually generating a saccade plan in response to the cue to move the eyes. An alternative explanation for the finding that saccades are faster when they are made in the direction instructed by the cue is that the saccadic reaction time difference reflects priming effects in the processing of the go signal, rather than differences in the extent of oculomotor preparation. Secondly, both elements of the dual task required a speeded response, and it is possible that participants prioritised the primary task, thus masking any effects in the secondary task (Hunt & Kingstone, 2003). A subsequent study by Hunt and Kingstone (2003) avoided this confound by using an unspeeded discrimination task to probe visual attention. They confirmed that the instruction to prepare a saccade facilitated subsequent eye-movements in the same direction, but did not facilitate visual perception for probes at the saccadic goal. However, saccadic reaction times

were again relatively slow (344 ms for saccades in the congruent condition), suggesting that the participants were not releasing a pre-programmed saccade.

These studies appear to offer evidence that saccade preparation is not required for endogenous attentional orienting. However, the extent to which endogenous attention depends on oculomotor preparation has remained controversial because of the ambiguity surrounding the extent to which participants were really preparing a saccadic eye-movement. An alternative approach to testing the Premotor theory that partially avoids this issue is to examine covert spatial attention in neuropsychological patients in whom oculomotor control is compromised in some way. If covert spatial attention depends on activation of the oculomotor system, the disruption to the oculomotor system caused by deficits of oculomotor control should result in abnormal spatial attention.

Experiments which have directly tested covert attention in patients with oculomotor problems have produced mixed results. Work by Rafal, Posner, Friedman, Inhoff and Bernstein (1988) with patients suffering from progressive supranuclear palsy (a disease that affects brain structures involved in saccade control) shows that these patients perform significantly more poorly on tasks that engage exogenous attention than those that require endogenous attention shifts, despite the primary oculomotor deficit being with initiation of voluntary rather than reflexive eye-movements. Similarly, patients with chronic lesions of the FEF have a saccadic deficit but no deficit of endogenous attention (Henik, Rafal, & Rhodes, 1994). More recently, Sereno, Briand, Amador & Szapiel (2006) described a single case with a lesion to the superior colliculus (SC) who showed abnormal reflexive eye-movements and unreliable exogenous attention in a peripheral cueing task (peripheral cueing

effects were only observed in two out of the four conditions where they would have been expected), suggesting that exogenous attention is dependent on oculomotor control. The patient also exhibited a deficit of Inhibition of Return (a bias against attending to previously peripherally cued locations)

Although the patient was not explicitly tested on endogenous attention, at long cue-target stimulus onset asynchronies (SOA) the patient showed a reliable facilitation at the cued location, perhaps suggesting that the patient's ability to endogenously orient attention was preserved. These findings demonstrate that lesions to the oculomotor system are not necessarily associated with a deficit of endogenous attention, and argue against the view that endogenous attention is dependent on activation of the oculomotor system.

In contrast, a study by Craighero, Carta & Fadiga (2001) appeared to show a direct link between oculomotor control and spatial attention. Specifically, they investigated endogenous attention in patients with a palsy of the VI<sup>th</sup> cranial nerve which impaired ocular motility on one eye, but left the other eye intact. Participants were shown a centrally presented cue (a pointer indicating left or right) which accurately predicted the location of a target on 70% of trials. Participants viewed the stimuli with the palsied eye and the intact eye in different conditions (the unused eye was patched). Consistent with the Premotor theory but not the findings of Klein and colleagues, endogenous attention was disrupted when viewing with the palsied eye but intact when viewing with the healthy eye. However, a subsequent study by Smith, Rorden & Jackson (2004) examined exogenous and endogenous attention in a patient (AI) with a complete, chronic ophthalmoplegia (paralysis of the eyes) affecting both

eyes. The deficit had been present since birth and the patient had never made a voluntary eye-movement. Endogenous attention was assessed using an arrow-cueing paradigm in which the cue correctly indicated target location on 80% of trials and exogenous attention was assessed using a non-predictive peripheral cueing paradigm. Contrary to the predictions of the Premotor theory AI showed completely intact endogenous attention. However, she did exhibit a subtle deficit of exogenous attention, such that peripheral cues no longer captured attention (although interestingly, AI did show intact Inhibition of Return, (Smith, Jackson, & Rorden, 2009))<sup>1</sup>. Similarly, Gabay Henik & Gradstein (2010) investigated exogenous and endogenous orienting in three patients with Duane's retraction syndrome, a chronic condition that reduces the motility of one of the eyes. As with VI<sup>th</sup> nerve palsy, only one eye is affected. Consistent with the previous findings of Smith et al., (2004) and Rafal et al., (1988), the ophthalmoplegia was associated with a deficit of exogenous orienting but, critically for the Premotor theory, no deficit of endogenous orienting.

The overall pattern of findings from patients with oculomotor problems is consistent with the conclusion that endogenous attention is not dependent on saccade preparation: in four out of five studies disruption to the oculomotor system leaves endogenous attention intact. The reason why endogenous attention is disrupted in the ophthalmoplegic patients studied by Craighero et al., (2001) but not in other ophthalmoplegic patients is not clear. However, one potentially important difference

---

<sup>1</sup> It has been argued by some authors that IOR can be used as a marker for exogenous attention, based on the assumption that IOR is caused by exogenous attention shift (e.g. Hunt & Kingstone 2003b). However, this assumption was not made by either Posner & Cohen (1984) or Klein (1999) in their theoretical accounts of IOR. In these accounts, IOR and covert attention are conceptualised as separate cognitive processes which are triggered by the same peripheral cue. This view of IOR is consistent with a growing body of empirical evidence showing that the inhibitory and facilitatory effects of peripheral cues can be dissociated experimentally (Danziger & Kingstone, 1999; Smith & Schenk, 2010; Tassinari, Aglioti, Chelazzi, Peru, & Berlucchi, 1994). We therefore argue that IOR is not necessarily a marker for a prior shift of attention, so studies measuring IOR but not early attentional facilitation cannot be used as evidence for or against the Premotor theory of attention.

between the patients is the duration of the ophthalmoplegia. Specifically, the patients described in Craighero et al., (2001) had a relatively acute ophthalmoplegia (patients were tested within 15 days of onset and recovered within 3-6 months) whereas patients in the other studies had chronic or degenerative conditions. One possibility is that patients with chronic ophthalmoplegia developed novel strategies for endogenous attentional orienting that allowed them to compensate for the damage to the oculomotor system. A related alternative possibility is suggested by recent work by Balslev, Gowen and Miall (2011). Balslev et al., (2011) demonstrated that repetitive TMS over cortical areas that process eye proprioceptive signals also biases visual perception, such that detection of low visibility targets is worse ipsilaterally and enhanced contralaterally. These data indicate that proprioceptive information about eye-position plays an important role in spatial attention. It is possible that the deficit of endogenous attention observed by Craighero was primarily driven by defective proprioceptive information about the position of the eye, rather than by problems preparing movements. The patients with chronic conditions may have been able to adapt their visual systems to compensate for the loss of the proprioceptive information about eye-position and thus preserve endogenous attentional orienting.

One major problem with all the studies of ophthalmoplegic patients is that although overt eye-movements are disrupted, it is impossible to know how the inability to execute a movement interacts with the ability to prepare a movement. In other words, although the participants have problems executing eye-movements, it is not possible to determine the extent to which the preparation of those eye-movements is disrupted. Proponents of the Premotor theory might justifiably argue that inability to execute a saccade is not equivalent to inability to plan a saccade, so at best the neuropsychological data is only weak evidence against the view that covert attention

depends upon motor preparation. A more rigorous test of the Premotor theory would be to measure endogenous attention under conditions where both saccade preparation and execution were impossible.

In order to provide this test Craighero, Nascimben & Fadiga (2004) developed an ingenious paradigm in which oculomotor preparation was prevented by manipulating the position of the eye. Participants fixated a stimulus array that was centred 40 degrees into the temporal hemifield (i.e. they were looking at the stimulus array out of the corner of the eye, with the other eye patched- see Figure 1). Targets were presented equidistantly from fixation, but participants could not plan or execute saccades to targets in the temporal hemispace because the target's location was beyond the oculomotor range.

**\*\*\*Figure 2 around here?\*\*\***

Craighero et al., (2004) reasoned that if the Premotor theory is correct, and covert attention depended on the ability to plan eye-movements, participants should experience attentional deficits at locations that could not become the goal of a saccade. Consistent with this hypothesis, participants exhibited normal cueing effects in response to a centrally presented, predictive cue in the nasal hemifield (to which saccades were possible), but no cueing effects in the temporal hemifield. Smith, Ball, Ellison & Schenk (2010) extended these results, using the same method to investigate the role of the eye-movement system in feature search. They found that easy, pop-out search was significantly slowed when the target appeared in the temporal hemifield, which was interpreted as a deficit of reflexive attention capture. When task difficulty was increased by making the distractors more heterogeneous and lowering the salience of the target, participants began to neglect targets such that detection

accuracy was significantly impaired in the temporal hemifield (search times were also slower, but this result was nonsignificant). Subsequently, Smith, Rorden & Schenk (in-press) demonstrated that abduction of the eye also produces a selective deficit of reflexive attention in the temporal hemispace using a peripheral cueing task, which is consistent with the view that exogenous attention is dependent on the ability to plan a saccade to the cued location (although interestingly, IOR was unaffected by the position of the eye). However, this study also included an endogenous cueing task in which attention was oriented in response to a centrally presented, predictive number cue. Contrary to the findings of Craighero et al., (2004), Smith et al., (in-press) observed no attentional deficit in the temporal hemispace and concluded that endogenous attention is independent of the oculomotor system.

It is not clear why eye-abduction should disrupt attention shifts generated by centrally presented spatial cues but not centrally presented non-spatial cues. One possibility is that spatial, directional cues actually primarily activate exogenous attention, rather than endogenous attentional mechanisms. Consistent with this interpretation, a number of studies have shown that arrow cues elicit the very rapid, mandatory shifts of attention (Bonato, Priftis, Marenzi, & Zorzi, 2009; Eimer, 1997; Hommel, Pratt, Colzato, & Godijn, 2001; Tipples, 2002, 2008) which are characteristic of exogenous attention. Furthermore, while the cues used by Craighero et al., (2004) were presented foveally, they were not presented centrally. More specifically, the cues were lines that suddenly appeared on either side of the central fixation point. These foveal but lateralised cues directly signalled target location, thus removing the need for participants to interpret the symbolic value of the cue. If the symbolic value of the cue did not need to be interpreted it is unlikely to have engaged endogenous attention. In this case, it is possible to reconcile the findings of Craighero

et al., (2004) with those of Smith et al. (in press) by proposing that in both studies the reduced cueing effect was due to disruption of the exogenous attentional mechanism.

Further evidence for the functional independence of covert attention and oculomotor control was provided by Juan and colleagues (Juan, Shorter-Jacobi, & Schall, 2004). In a very elegant study they had monkeys perform an eye-movement task which required the animal to attend to the orientation of a peripherally presented colour singleton, then make a pro- or anti- saccade based on the orientation of this singleton. Microstimulation of FEF was used to evoke eye-movements at different times relative to the appearance of the singleton. Juan et al., reasoned that if covert attention was equivalent to the activation of a saccade plan, the saccade plan associated with attending to the colour singleton should interfere with the saccade being evoked by microstimulation. This interference would manifest as deviations in the trajectory of the evoked saccade towards the attended location. In contrast to this prediction they observed no evidence that evoked saccades were deviated towards the locus of attention when saccades were evoked in the first 120 ms of stimulus presentation (the time in which FEF activity is known to be related to the processing of the identity of the colour singleton; Sato and Schall 2003). This data suggests that covert attention to a colour singleton is not contingent on the activation of a saccade plan (at least, not in FEF). One might object that (a) visual selection by FEF neurons in a primate may not be functionally equivalent to a covert shift of attention in a human and (b) there was no objective measure of attentional allocation in Juan's study, so they do not really know where the monkey was attending. In this case, generalisations about the role of oculomotor preparation based on experiments in monkeys need to be treated with caution. To address this issue, Smith & Schenk (2007) used a similar antisaccade task to probe the role of saccade preparation in

covert attention in humans. In this task participants were presented with an array of items, one of which was a colour singleton. They were asked to make pro- or anti saccades depending on the orientation of the singleton. To measure attention, a briefly presented discrimination probe was presented during the first 120 ms of each trial (i.e. the time in which visual selection but no saccade preparation was observed in monkeys). Critically, on antisaccade trials (where locus of attention was dissociated from saccade endpoint) attentional facilitation was observed when the probe appeared at the colour singleton, but not when it appeared at the saccade goal, confirming that the singleton was attended and that attentional selection is possible in the absence of saccade preparation. Juan, Muggleton, Tzeng, Hung, Cowey & Walsh (2008) subsequently demonstrated that the dissociation between oculomotor preparation and attention observed in monkey FEF could also be observed in humans. Participants were shown stimulus arrays similar to those used by Juan et al., (2004) and asked to make pro or anti saccades based on the orientation of the singleton. TMS was delivered over FEF at different time-points following the onset of the stimulus array. It was found that TMS disrupted saccade latency when delivered 40-80 ms after array onset (i.e. during visual selection but not saccade preparation), and again when delivered 200 ms before saccade onset (i.e. at the start of movement preparation but after visual selection), demonstrating a temporal dissociation between visual selection and saccade preparation in the human FEF. Together, these studies offer compelling evidence against the view that saccade preparation is necessary for covert spatial attention.

To summarize, the Premotor theory predicts functional equivalence between motor preparation and covert attention, such that the preparation of a goal directed action is not only sufficient but also a necessary precondition for a covert shift of

attention. Contrary to this prediction, endogenous oculomotor preparation does not facilitate perception at the saccade goal, endogenous attention is not associated with the mandatory activation of a saccade plan in humans or primates, and lesions to the oculomotor system create a deficit of exogenous attention but generally leave endogenous attention intact. These results provide converging evidence that endogenous attention is not dependent of the activation of a motor plan, and suggest that the Premotor hypothesis of functional equivalence between motor preparation and covert endogenous attention should be rejected.

## **5. An alternative theoretical framework**

The studies described in this review show that there is a tight coupling between attention and saccade planning, but cannot demonstrate a causal link between the two. There is evidence that activating monkey FEF using microstimulation is sufficient to bias attention (Armstrong et al., 2006; Armstrong & Moore, 2007; Moore & Armstrong, 2003; Moore & Fallah, 2001), but this bias is unlikely to originate from the specific activation of neurons involved in motor preparation as compelling neurophysiological evidence suggests that covert attention and saccade control are mediated by separate neuronal populations in FEF (Juan et al., 2008; Juan et al., 2004; Sato & Schall, 2003; Thompson et al., 1997; Thompson et al., 2005). Furthermore, it is probable that the perceptual enhancements observed at saccade goals prior to saccade execution are driven by the mechanisms which ensure the maintenance of perceptual stability which do not operate when no saccade is executed (Duhamel et

al., 1992; Khan et al., 2009). Consistent with this proposal, studies where human observers prepare but withhold saccades find no evidence of attentional facilitation at the saccade goal (Hunt & Kingstone, 2003; Klein, 1980; Klein & Pontefract, 1994). In addition, patients with lesions to the FEF have problems with saccadic eye-movements but no deficit of covert endogenous attention (Henik et al., 1994). There was evidence from one study that patients who are unable to execute eye-movements experience deficits of endogenous attention (Craighero et al., 2001) but many other studies consistently report preserved endogenous attention but disrupted exogenous attention in ophthalmoplegic patients (Gabay et al., 2010; Rafal et al., 1988; Smith et al., 2004). The strongest evidence for a causal link between saccade preparation and covert attention comes from a study using the eye-abduction technique, which shows that preventing saccade preparation by placing the eye at the limit of the oculomotor range elicits deficits of endogenous attention (Craighero et al., 2004). However, this study used a direction cue which may be dependent on exogenous attentional mechanisms. Consistent with this explanation a later study that attempted to replicate the effect using a symbolic number cue to endogenously orient attention did not find a deficit of endogenous attention (although exogenous attention was disrupted) (Smith et al., in-press). Taken together, these studies provide compelling converging evidence that endogenous attention is independent of oculomotor activation, and are clearly contrary to the predictions of the Premotor theory. The evidence for functional equivalence between saccade preparation and exogenous attention is more persuasive, as lesions to the oculomotor system cause systematic and reliable deficits of exogenous orienting (Gabay et al., 2010; Rafal et al., 1988; Sereno et al., 2006; Smith et al., 2010; Smith et al., 2004; Smith et al., in-press). Given these conclusions, the strong claim that all covert shifts of spatial attention depend on activation of saccade

plans should be rejected. However, a conservative version of the Premotor theory in which only exogenous attention is dependent on motor preparation may still be tenable. A conservative Premotor theory fits well with the existing empirical data showing that (a) damage to the oculomotor system generally leaves endogenous attention intact, but severely disrupts exogenous attention and (b) the intention to make a saccade is not sufficient to orient attention.

A reduced version of the Premotor theory can be accommodated within a broader theoretical framework developed to account for both spatial and non-spatial visual attention. More specifically, the biased competition (BC) account of visual attention (Desimone, 1998; Desimone & Duncan, 1995; Duncan, 1998) proposes that attention is the consequence of competition within and across different sensory-motor systems. In this view, sensory inputs compete for neural representation within sensory and motor systems. The more physically salient an input is, the greater its representation. The competition between representations is integrated across sensory and motor systems so that different systems converge on a single representation. This representation is the ‘winner’ of the competition and is attended, in the sense that it becomes available to higher cognitive processes such as awareness and response systems. Critically, competition can be biased towards less physically salient stimuli by top down factors such as our current goals and the content of working memory (Soto, Hodsoll, Rotshtein, & Humphreys, 2008).

During exogenous cueing the sudden appearance of the cue briefly increases the physical salience of the cued location and triggers the preparation of a saccade, creating a powerful bias in the visual and oculomotor system towards the cued location. This bias propagates through the perceptual-motor system and facilitates

processing of subsequent visual events at the cued location (i.e. the cued location becomes attended). However, when the ability to represent spatial locations as the goal of a movement is compromised, either by a lesion to the oculomotor system or an experimental manipulation, such as eye-abduction, the onset of the cue does not create a bias in the oculomotor system. As a consequence, visual events from the cued location are not prioritized in the visuomotor system so no cueing effect is observed. In contrast, during an endogenous cueing task the participant knows that the cue accurately predicts target location and can use top-down cognitive processes that are independent of the eye-movement system to bias the visual system toward the cued location. Lesions to the oculomotor system are therefore unlikely to disrupt endogenous attentional orienting because they typically spare the parts of the cognitive system involved in the top-down control of behaviour. When top-down biases are in competition with biases from the motor system, the extent to which any location will be attended will depend on the relative strength of the biases generated by the motor and cognitive system. When the motor signal is dominant (e.g. in the moments prior to a saccade or limb movement) activity in the cognitive system converges on the movement goal and sensory signal from this location are attended. However, when there is competition between equally powerful signals in both the cognitive system and the motor system (e.g. when a saccade is planned but unexecuted to one location and a target is expected to appear at a different location) the signal from the motor endpoint may not be strong enough to bias the processing of the action endpoint. In this view, motor preparation increases the probability that a location will be attended, but does not guarantee it.

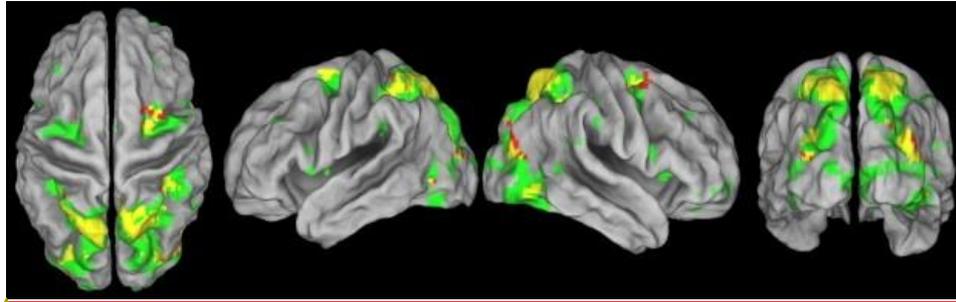
One might argue that a model of attention based on BC would predict a single locus of attention, yet there appears to be evidence of multiple attentional foci at

different motor endpoints (Jonikaitis & Deubel, 2011). The Premotor theory makes no such prediction so better accounts for these data. However, it is important to carefully consider both the predictions of BC and the findings of these studies. BC argues that when multiple signals are present they compete until a single signal dominates the others. Critically, the probability of any specific signal winning the competition will vary on a trial-by-trial basis. For example, if an observer is planning a saccade to one location but a reach to a different location, on some trials the motor plan might win the competition and on other trials the reach plan might win. In the study that shows multiple attentional foci, (Jonikaitis & Deubel, 2011) the presence of attention is inferred from enhanced performance at movement goals relative to 'neutral' locations to which the observer not planning an action. If one assumes that the saccade goal and the reach goal are equally likely to win the competition, then on half the trials the reach goal will be attended and on the other half the saccade goal will be attended. Over the course of hundreds of trials this single, variable locus of attention would produce better performance at both endpoints relative to the unattended locations, and give the illusion of parallel attentional selection of the two endpoints. Note that they also found that combined reaches and saccades to the same location produced greater attentional facilitation than reaches or saccades alone, but this would be expected as now the movement endpoint is attended on every trial, not a proportion of trials.

## **6. Conclusions**

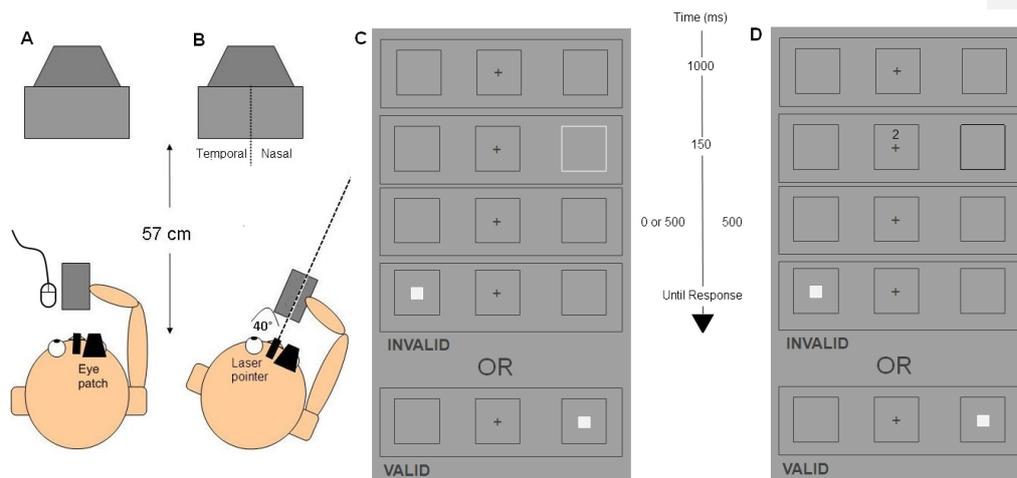
The Premotor theory argues that spatial attention emerges from activation of motor plans, such that motor preparation is both necessary and sufficient for shifts of spatial attention. We have shown that the strongest evidence for this hypothesis- the mandatory coupling of attention to the goals of eye-movements in the moments before saccade onset- can be accounted for in terms of neural mechanisms (spatial remapping) that are only active in the case of overt but not covert attentional shifts. The spatial-remapping account therefore assumes that oculomotor preparation is linked to overt but not covert shifts of attention. Studies that examine covert shifts of attention (i.e. attentional shifts unaccompanied by saccadic movements) typically demonstrate independence between endogenous attention and motor preparation but a much tighter coupling between exogenous attention and motor preparation, such that inability to prepare actions creates a deficit of reflexive attention. These data are consistent with a limited version of the Premotor theory in which saccade preparation is necessary for exogenous attentional orienting, whereas endogenous attentional orienting is entirely independent of motor control. However, we propose that the relationship between motor control and spatial attention is better understood in terms of a biased competition model of the cognitive system, in which activity in the motor system contributes to competition between different sensory representations. Action preparation can increase the probability of the goal of the action being selected for processing, but it cannot guarantee it, and the absence of motor preparation does not prevent a location from being attended. If the biased competition model is correct, the challenge for researchers is to more completely characterise the complex interactions between different cognitive systems that give rise to spatial attention.

Figures:



**Formatted:** Font: Bold, Font color: Black

**Figure 1:** Overlapping neural activations during overt saccades and covert spatial attention. The areas of the brain significantly activated in the covert shift of attention task are shown in red. The areas of the brain significantly activated in the overt shift of attention task are shown in green. The areas of the brain activated in both the overt and the covert shift of attention task are shown in yellow (Source, de Haan, B., Moryan, P. S., & Rorden, C. (2008). Covert orienting of attention and overt eye movements activate identical brain regions. *Brain Research*, 1204, 102-111. Reproduced with permission. Elsevier)



**Figure 2:** Illustration of the eye-abduction paradigm. Panel A shows the canonical 'frontal' position, where the viewing eye is in the centre of the orbit. Participants are instructed to fixate but can still prepare movements to nasal and temporal hemifields. Panel B shows the abducted position in which the viewing eye is abducted by 40 degrees away from the body midline (i.e. the limit of the oculomotor range). In this eye-abducted condition the participant can no longer make (and presumably does not plan) saccades into the temporal hemifield. This, therefore, provides a test of the pre-motor theory. The pre-motor theory would predict that in this condition participants will also be unable to shift their attention into the temporal hemifield. Smith, Schenk & Rorden (in press) tested this idea for an exogenous (C) and endogenous (D) cueing task and found that eye-abduction interferes with exogenous but not with endogenous attention shifts.

## References

- Andersen, R. A., Snyder, L. H., Batista, A. P., Buneo, C. A., & Cohen, Y. E. (1998). Posterior parietal areas specialized for eye movements (LIP) and reach (PRR) using a common coordinate frame. In *Sensory Guidance of Movement* (Vol. 218, pp. 109-128).
- Armstrong, K. M., Fitzgerald, J. K., & Moore, T. (2006). Changes in Visual Receptive Fields with Microstimulation of Frontal Cortex. *Neuron*, *50*(5), 791-798.
- Armstrong, K. M., & Moore, T. (2007). Rapid enhancement of visual cortical response discriminability by microstimulation of the frontal eye field. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(22), 9499-9504.
- Baldauf, D., & Deubel, H. (2008a). Properties of attentional selection during the preparation of sequential saccades. *Experimental Brain Research*, *184*(3), 411-425.
- Baldauf, D., & Deubel, H. (2008b). Visual attention during the preparation of bimanual movements. *Vision Research*, *48*(4), 549-563.
- Baldauf, D., & Deubel, H. (2009). Attentional Selection of Multiple Goal Positions Before Rapid Hand Movement Sequences: An Event-related Potential Study. *Journal of Cognitive Neuroscience*, *21*(1), 18-29.
- Baldauf, D., Wolf, M., & Deubel, H. (2006). Deployment of visual attention before sequences of goal-directed hand movements. *Vision Research*, *46*(26), 4355-4374.
- Balslev, D., Gowen, E., & Miall, R. C. (2011). Decreased Visual Attention Further from the Perceived Direction of Gaze for Equidistant Retinal Targets. *Journal of Cognitive Neuroscience*, *23*(3), 661-669.
- Beauchamp, M. S., Petit, L., Ellmore, T. M., Ingelholm, J., & Haxby, J. V. (2001). A parametric fMRI study of overt and covert shifts of visuospatial attention. *Neuroimage*, *14*(2), 310-321.
- Beckers, G., Canavan, A. G. M., Zangemeister, W. H., & Homberg, V. (1992). Transcranial Magnetic Stimulation of Human Frontal and Parietal Cortex Impairs Programming of Periodic Saccades. *Neuro-Ophthalmology*, *12*(5), 289-295.
- Bisley, J. W., & Goldberg, M. E. (2003). Neuronal activity in the lateral intraparietal area and spatial attention. *Science*, *299*(5603), 81-86.
- Bisley, J. W., & Goldberg, M. E. Attention, Intention, and Priority in the Parietal Lobe. In *Annual Review of Neuroscience*, Vol 33 (Vol. 33, pp. 1-21). Palo Alto: Annual Reviews.
- Bonato, M., Priftis, K., Marenzi, R., & Zorzi, M. (2009). Normal and Impaired Reflexive Orienting of Attention after Central Nonpredictive Cues. *Journal of Cognitive Neuroscience*, *21*(4), 745-759.
- Bonfiglioli, C., Duncan, J., Rorden, C., & Kennett, S. (2002). Action and perception: Evidence against converging selection processes. *Visual Cognition*, *9*(4-5), 458-476.
- Bushnell, M. C., Goldberg, M. E., & Robinson, D. L. (1981). Behavioral Enhancement of Visual Responses in Monkey Cerebral- Cortex .1. Modulation in Posterior Parietal Cortex Related to Selective Visual-Attention. *Journal of Neurophysiology*, *46*(4), 755-772.

- Chambers, C. D., Payne, J. M., & Mattingley, J. B. (2007). Parietal disruption impairs reflexive spatial attention within and between sensory modalities. *Neuropsychologia*, *45*(8), 1715-1724.
- Chambers, C. D., Stokes, M. G., & Mattingley, J. B. (2004). Modality-specific control of strategic spatial attention in parietal cortex. *Neuron*, *44*(6), 925-930.
- Chambers, C. D., Payne, J. M., Stokes, M. G., & Mattingley, J. B. (2004). Fast and slow parietal pathways mediate spatial attention. *Nature Neuroscience*, *7*(3), 217-218.
- Colby, C. L., Duhamel, J. R., & Goldberg, M. E. (1996). Visual, presaccadic, and cognitive activation of single neurons in monkey lateral intraparietal area. *J Neurophysiol*, *76*(5), 2841-2852.
- Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., et al. (1998). A common network of functional areas for attention and eye movements. *Neuron*, *21*(4), 761-773.
- Craighero, L., Carta, A., & Fadiga, L. (2001). Peripheral oculomotor palsy affects orienting of visuospatial attention. *NeuroReport*, *12*(15), 3283-3286.
- Craighero, L., Nascimben, M., & Fadiga, L. (2004). Eye position affects orienting of visuospatial attention. *Current Biology*, *14*(4), 331-333.
- de Haan, B., Moryan, P. S., & Rorden, C. (2008). Covert orienting of attention and overt eye movements activate identical brain regions. *Brain Research*, *1204*, 102-111.
- Danziger, S., & Kingstone, A. (1999). Unmasking the inhibition of return phenomenon. *Perception & Psychophysics*, *61*(6), 1024-1037.
- Desimone, R. (1998). Visual attention mediated by biased competition in extrastriate visual cortex. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, *353*(1373), 1245-1255.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 192-222.
- Deubel, H. (2008). The time course of presaccadic attention shifts. *Psychological Research-Psychologische Forschung*, *72*(6), 630-640.
- Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, *36*(12), 1827-1837.
- Deubel, H., & Schneider, W. X. (2003). Delayed saccades, but not delayed manual aiming movements, require visual attention shifts. In *Oculomotor and Vestibular Systems: Their Function and Disorders* (Vol. 1004, pp. 289-296).
- Deubel, H., Schneider, W. X., & Paprotta, I. (1998). Selective dorsal and ventral processing: Evidence for a common attentional mechanism in reaching and perception. *Visual Cognition*, *5*(1-2), 81-107.
- Dore-Mazars, K., Pouget, P., & Beauvillain, C. (2004). Attentional selection during preparation of eye movements. *Psychological Research-Psychologische Forschung*, *69*(1-2), 67-76.
- Duhamel, J.-R., Colby, C. L., & Goldberg, M. E. (1992). The Updating of the Representation of Visual Space in Parietal Cortex by Intended Movements. *Science*, *255*, 90-92.
- Duncan, J. (1998). Converging levels of analysis in the cognitive neuroscience of visual attention. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, *353*, 1307-1317.

- Eimer, M. (1997). Uninformative symbolic cues may bias visual-spatial attention: Behavioral and electrophysiological evidence. *Biological Psychology*, 46(1), 67-71.
- Eimer, M., Forster, B., Van Velzen, J., & Prabhu, G. (2005). Covert manual response preparation triggers attentional shifts: ERP evidence for the premotor theory of attention. *Neuropsychologia*, 43(6), 957-966.
- Ellison, A., Rushworth, M., & Walsh, V. (2003). The parietal cortex in visual search: A visuomotor hypothesis. *Supplements to Clinical Neurophysiology*(56), 321-330.
- Ellison, A., Schindler, I., Pattison, L. L., & Milner, A. D. (2004). An exploration of the role of the superior temporal gyrus in visual search and spatial perception using TMS. *Brain*, 127, 2307-2315.
- Fecteau, J. H., & Munoz, D. P. (2006). Saliency, relevance, and firing: a priority map for target selection. *Trends in Cognitive Sciences*, 10(8), 382-390.
- Fischer, M. H. (1997). Attention allocation during manual movement preparation and execution. *European Journal of Cognitive Psychology*, 9(1), 17-51.
- Gabay, S., Henik, A., & Gradstein, L. (2010). Ocular motor ability and covert attention in patients with Duane Retraction Syndrome. *Neuropsychologia*, 48(10), 3102-3109.
- Gaymard, B., Ploner, C. J., Rivaud, S., Vermersch, A. I., & Pierrot-Deseilligny, C. (1998). Cortical control of saccades. *Experimental Brain Research*, 123(1-2), 159-163.
- Gherri, E., & Eimer, M. (2010). Manual response preparation disrupts spatial attention: An electrophysiological investigation of links between action and attention. *Neuropsychologia*, 48(4), 961-969.
- Godijn, R., & Theeuwes, J. (2003). Parallel allocation of attention prior to the execution of saccade sequences. *Journal of Experimental Psychology-Human Perception and Performance*, 29(5), 882-896.
- Grosbras, M.-H., & Paus, T. (2002). Transcranial Magnetic Stimulation of the Human Frontal Eye Field: Effects on Visual Perception and Attention. *Journal of Cognitive Neuroscience*, 14(7), 1109-1120.
- Henik, A., Rafal, R., & Rhodes, D. (1994). Endogenously Generated and Visually Guided Saccades after Lesions of the Human Frontal Eye Fields. *Journal of Cognitive Neuroscience*, 6(4), 400-411.
- Hoffman, J. E., & Subramaniam, B. (1995). The Role of Visual-Attention in Saccadic Eye-Movements. *Perception & Psychophysics*, 57(6), 787-795.
- Hommel, B., Pratt, J., Colzato, L., & Godijn, R. (2001). Symbolic control of visual attention. *Psychological Science*, 12(5), 360-365.
- Hunt, A. R., & Kingstone, A. (2003a). Covert and overt voluntary attention: linked or independent? *Cognitive Brain Research*, 18(1), 102-105.
- Hunt, A. R., & Kingstone, A. (2003b). Inhibition of return: Dissociating attentional and oculomotor components. *Journal of Experimental Psychology-Human Perception and Performance*, 29(5), 1068-1074.
- Jonides, J. (1981). Voluntary vs reflexive control of the mind's eye's movement. In D. Baddeley (Ed.), *Attention and Performance IX*. Hillsdale: Lawrence Erlbaum.
- Jonikaitis, D., & Deubel, H. (2011). Independent Allocation of Attention to Eye and Hand Targets in Coordinated Eye-Hand Movements. *Psychological Science*, 22(3), 339-347.

- Juan, C. H., Muggleton, N. G., Tzeng, O. J. L., Hung, D. L., Cowey, A., & Walsh, V. (2008). Segregation of visual selection and saccades in human frontal eye fields. *Cerebral Cortex*, *18*(10), 2410-2415.
- Juan, C. H., Shorter-Jacobi, S. M., & Schall, J. D. (2004). Dissociation of spatial attention and saccade preparation. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(43), 15541-15544.
- Khan, A. Z., Blangero, A., Rossetti, Y., Salemme, R., Luaute, J., Deubel, H., et al. (2009). Parietal Damage Dissociates Saccade Planning from Presaccadic Perceptual Facilitation. *Cerebral Cortex*, *19*(2), 383-387.
- Khan, A. Z., Song, J. H., & McPeck, R. M. (2011). The eye dominates in guiding attention during simultaneous eye and hand movements. *Journal of Vision*, *11*(1).
- Klein, R. (2009). On the Control of Attention. *Canadian Journal of Experimental Psychology-Revue Canadienne De Psychologie Experimentale*, *63*(3), 240-252.
- Klein, R. M. (1980). Does Oculomotor readiness mediate cognitive control of visual attention? In R. Nickerson (Ed.), *Attention and Performance* (Vol. IX, pp. 259-276). Hillsdale: Erlbaum.
- Klein, R. M., & MacInnes, W. J. (1999). Inhibition of return is a foraging facilitator in visual search. *Psychological Science*, *10*(4), 346-352.
- Klein, R. M., & Pontefract, A. (1994). Does Oculomotor Readiness Mediate Cognitive Control of Visual-Attention - Revisited. In *Attention and Performance Xv* (Vol. 15, pp. 333-350). Cambridge: MIT PRESS.
- Kowler, E., Anderson, E., Doshier, B., & Blaser, E. (1995). The Role of Attention in the Programming of Saccades. *Vision Research*, *35*(13), 1897-1916.
- Lane, A. R., Smith, D. T., Schenk, T., & Ellison, A. (2011). The Involvement of Posterior Parietal Cortex in Feature and Conjunction Visuomotor Search. *Journal of Cognitive Neuroscience*, *23*(8), 1964-1972.
- Montagnini, A., & Castet, E. (2007). Spatiotemporal dynamics of visual attention during saccade preparation: Independence and coupling between attention and movement planning. *Journal of Vision*, *7*(14).
- Moore, T., & Armstrong, K. M. (2003). Selective gating of visual signals by microstimulation of frontal cortex. *Nature*, *421*(6921), 370-373.
- Moore, T., Armstrong, K. M., & Fallah, M. (2003). Visuomotor origins of covert spatial attention. *Neuron*, *40*(4), 671-683.
- Moore, T., & Fallah, M. (2001). Control of eye movements and spatial attention. *Proceedings of the National Academy of Science*, *98*(3), 1273-1276.
- Muggleton, N. G., Juan, C. H., Cowey, A., & Walsh, V. (2003). Human frontal eye fields and visual search. *Journal of Neurophysiology*, *89*(6), 3340-3343.
- Muller, H. J., & Rabbitt, P. M. A. (1989). Reflexive and Voluntary Orienting of Visual-Attention - Time Course of Activation and Resistance to Interruption. *Journal of Experimental Psychology-Human Perception and Performance*, *15*(2), 315-330.
- Muri, R. M., Hess, C. W., & Meienberg, O. (1991). Transcranial Stimulation of the Human Frontal Eye Field by Magnetic Pulses. *Experimental Brain Research*, *86*(1), 219-223.
- Muri, R. M., Vermersch, A. I., Rivaud, S., Gaymard, B., & PierrotDeseilligny, C. (1996). Effects of single-pulse transcranial magnetic stimulation over the prefrontal and posterior parietal cortices during memory-guided saccades in humans. *Journal of Neurophysiology*, *76*(3), 2102-2106.

- Nakamura, K., & Colby, C. L. (2002). Updating of the visual representation in monkey striate and extrastriate cortex during saccades. *Proceedings of the National Academy of Sciences of the United States of America*, 99(6), 4026-4031.
- Nobre, A. C., Gitelman, D. R., Dias, E. C., & Mesulam, M. M. (2000). Covert visual spatial orienting and saccades: Overlapping neural systems. *Neuroimage*, 11(3), 210-216.
- O'Shea, J., Muggleton, N. G., Cowey, A., & Walsh, V. (2004). Timing of target discrimination in human frontal eye fields. *Journal of Cognitive Neuroscience*, 16(6), 1060-1067.
- Perry, R. J., & Zeki, S. (2000). The neurology of saccades and covert shifts in spatial attention - An event-related fMRI study. *Brain*, 123, 2273-2288.
- Peterson, M., Kramer, A., & Irwin, D. (2004). Covert shifts of attention precede involuntary eye movements. *Attention Perception & Psychophysics*, 66(3), 398-405.
- Posner, M. I. (1980). Orienting of Attention. *Quarterly Journal of Experimental Psychology*, 32(FEB), 3-25.
- Posner, M. I., & Cohen, Y. (1984). Components of Visual Orienting. In H. Bouma & D. Bouwhuis (Eds.), *Attention and Performance X* (pp. 531-556). London: Erlbaum Associates.
- Posner, M. I., Rafal, R. D., Choate, L. S., & Vaughan, J. (1985). Inhibition of Return - Neural Basis and Function. *Cognitive Neuropsychology*, 2(3), 211-228.
- Rafal, R. D., Posner, M. I., Friedman, J. H., Inhoff, A. W., & Bernstein, E. (1988). Orienting of Visual-Attention in Progressive Supranuclear Palsy. *Brain*, 111, 267-280.
- Rizzolatti, G., Riggio, L., Dascola, I., & Umiltà, C. (1987). Reorienting Attention across the Horizontal and Vertical Meridians - Evidence in Favor of a Premotor Theory of Attention. *Neuropsychologia*, 25(1A), 31-40.
- Rizzolatti, G., Riggio, L., & Sheliga, B. M. (1994). Space and Selective Attention. In *Attention and Performance Xv* (Vol. 15, pp. 231-265).
- Rorden, C., & Driver, J. (1999). Does auditory attention shift in the direction of an upcoming saccade? *Neuropsychologia*, 37(3), 357-377.
- Rorden, C., Greene, K., Sasine, G. M., & Baylis, G. C. (2002). Enhanced tactile performance at the destination of an upcoming saccade. *Current Biology*, 12(16), 1429-1434.
- Ruff, C. C., Bestmann, S., Blankenburg, F., Bjoertomt, O., Josephs, O., Weiskopf, N., et al. (2008). Distinct causal influences of parietal versus frontal areas on human visual cortex: Evidence from concurrent TMS-fMRI. *Cerebral Cortex*, 18(4), 817-827.
- Ruff, C. C., Blankenburg, F., Bjoertomt, O., Bestmann, S., Freeman, E., Haynes, J.-D., et al. (2006). Concurrent TMS-fMRI and psychophysics reveal frontal influences on human retinotopic visual cortex. *Current Biology*, 16(15), 1479-1488.
- Sack, A. T., Hubl, D., Prvulovic, D., Formisano, E., Jandl, M., Zanella, F. E., et al. (2002). The experimental combination of rTMS and fMRI reveals the functional relevance of parietal cortex for visuospatial functions. *Cognitive Brain Research*, 13(1), 85-93.
- Sato, T. R., & Schall, J. D. (2003). Effects of stimulus-response compatibility on neural selection in frontal eye field. *Neuron*, 38(4), 637-648.

- Schiegg, A., Deubel, H., & Schneider, W. X. (2003). Attentional selection during preparation of prehension movements. *Visual Cognition, 10*(4), 409-431.
- Schindler, I., Ellison, A., & Milner, A. D. (2008). Contralateral visual search deficits following TMS. *Journal of Neuropsychology, 2*, 501-508.
- Schneider, W. X. (1995). VAM: A neuro-cognitive model for visual attention control of segmentation, object recognition, and space-based motor action. *Visual Cognition, 2*(2), 331 - 376.
- Schneider, W. X., & Deubel, H. (2002). Selection-for-perception and selection-for-spatial-motor-action are coupled by visual attention: a review of recent findings and new evidence from stimulus-driven saccade control. *Common Mechanisms in Perception and Action, 19*, 609-627.
- Sereno, A. B., Briand, K. A., Amador, S. C., & Szapiel, S. V. (2006). Disruption of reflexive attention and eye movements in an individual with a collicular lesion. *Journal of Clinical and Experimental Neuropsychology, 28*(1), 145-166.
- Shepherd, M., Findlay, J. M., & Hockey, R. J. (1986). The Relationship between Eye-Movements and Spatial Attention. *Quarterly Journal of Experimental Psychology Section a-Human Experimental Psychology, 38*(3), 475-491.
- Silvanto, J., Lavie, N., & Walsh, V. (2006). Stimulation of the human frontal eye fields modulates sensitivity of extrastriate visual cortex. *Journal of Neurophysiology, 96*(2), 941-945.
- Smith, D. T., Ball, K., Ellison, A., & Schenk, T. (2010). Deficits of reflexive attention induced by abduction of the eye. *Neuropsychologia, 48*, 1269-1276.
- Smith, D. T., Jackson, S. R., & Rorden, C. (2005). Transcranial magnetic stimulation of the left human frontal eye fields eliminates the cost of invalid endogenous cues. *Neuropsychologia, 43*(9), 1288-1296.
- Smith, D. T., Jackson, S. R., & Rorden, C. (2009). An intact eye-movement system is not required to generate Inhibition of Return. *Journal of Neuropsychology*(3), 267-271.
- Smith, D. T., Jackson, S. R., & Rorden, C. (2009). Repetitive TMS over frontal eye fields disrupts visually cued auditory attention. *Brain Stimulation, 2*, 81-87.
- Smith, D. T., Rorden, C., & Jackson, S. R. (2004). Exogenous orienting of attention depends upon the ability to execute eye movements. *Current Biology, 14*(9), 792-795.
- Smith, D. T., Rorden, C., & Schenk, T. (in press). Saccade preparation is required for exogenous attention but not endogenous attention or IOR. *Journal of Experimental Psychology-Human Perception and Performance*
- Smith, D. T., & Schenk, T. (2007). Enhanced probe discrimination at the location of a colour singleton. *Experimental Brain Research, 181*(2), 367-375.
- Smith, D. T., & Schenk, T. (2010). Inhibition of Return exaggerates change blindness. *Quarterly Journal of Experimental Psychology, 63*(11), 2231-2238.
- Soto, D., Hodsoll, J., Rotshtein, P., & Humphreys, G. W. (2008). Automatic guidance of attention from working memory. *Trends in Cognitive Sciences, 12*(9), 342-348.
- Tassinari, G., Aglioti, S., Chelazzi, L., Peru, A., & Berlucchi, G. (1994). Do peripheral non-informative cues induce early facilitation of target detection. *Vision Research, 34*(2), 179-189.
- Taylor, P. C. J., Nobre, A. C., & Rushworth, M. F. S. (2007). FEF TMS affects visual cortical activity. *Cerebral Cortex, 17*(2), 391-399.

- Tehovnik, E. J. (1996). Electrical stimulation of neural tissue to evoke behavioral responses. *Journal of Neuroscience Methods*, 65(1), 1-17.
- Thickbroom, G. W., Stell, R., & Mastaglia, F. L. (1996). Transcranial magnetic stimulation of the human frontal eye field. *Journal of the Neurological Sciences*, 144(1-2), 114-118.
- Thompson, K. G., Bichot, N. P., & Schall, J. D. (1997). Dissociation of visual discrimination from saccade programming in macaque frontal eye field. *Journal of Neurophysiology*, 77(2), 1046-1050.
- Thompson, K. G., Biscoe, K. L., & Sato, T. R. (2005). Neuronal basis of covert spatial attention in the frontal eye field. *Journal of Neuroscience*, 25(41), 9479-9487.
- Tipples, J. (2002). Eye gaze is not unique: Automatic orienting in response to uninformative arrows. *Psychonomic Bulletin & Review*, 9(2), 314-318.
- Tipples, J. (2008). Orienting to counterpredictive gaze and arrow cues. *Perception & Psychophysics*, 70(1), 77-87.
- Van der Stigchel, S., & Theeuwes, J. (2005). The influence of attending to multiple locations on eye movements. *Vision Research*, 45(15), 1921-1927.
- Wurtz, R. H., & Mohler, C. W. (1976). Enhancement of visual responses in monkey striate cortex and frontal eye fields. *Journal of Neurophysiology*, 39(4), 766-772.
- Zangemeister, W. H., Canavan, A. G. M., & Hoemberg, V. (1995). Frontal and Parietal Transcranial Magnetic Stimulation (TMS) Disturbs Programming of Saccadic Eye-Movements. *Journal of the Neurological Sciences*, 133(1-2), 42-52.