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Covert attention beyond the range of eye-movements: Evidence for a dissociation between exogenous and endogenous orienting



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ABSTRACT

The relationship between covert shift of attention and the oculomotor system has been the subject of numerous studies. A widely held view, known as Premotor Theory, is that covert attention depends upon activation of the oculomotor system. However, recent work has argued that Premotor Theory is only true for covert, exogenous orienting of attention and that covert endogenous orienting is largely independent of the oculomotor system. To address this issue we examined how endogenous and exogenous covert orienting of attention was affected when stimuli were presented at a location outside the range of saccadic eye movements. Results from Experiment 1 showed that exogenous covert orienting was abolished when stimuli were presented beyond the range of saccadic eye movements, but preserved when stimuli were presented within this range. In contrast, in Experiment 2 endogenous covert orienting was preserved when stimuli appeared beyond the saccadic range. Finally, Experiment 3 confirmed the observations of Exp.1 and 2. Our results demonstrate that exogenous, covert orienting is limited to the range of overt saccadic eye movements, whereas covert endogenous orienting is not. These results are consistent with a weak, exogenous-only version of Premotor Theory.

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1. Introduction

Every day we are faced with numerous visual inputs that our visual system needs to filter in order to select the information of interest. This selection can be driven endogenously, by our current goals and desires, or exogenously, in response to salient visual events in the environment (Posner & Cohen, 1980). Under normal circumstances this visual selection is achieved by making a saccadic eye movement that places the

object or location of interest on the fovea, thus greatly enhancing the perception of fine detail. These 'overt' shifts of attention are always preceded by transient enhancement of perception at the saccade goal which is only observed in the moments before saccade onset (Deubel & Schneider, 1996; Shepherd, Findlay, & Hockey, 1986). This process of target selection that precede the saccade triggering can be referred to as 'selection for action' processes (Schneider, 1995; Schneider & Deubel, 2002). However, it is also possible to

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orient attention without making any overt eye movements at all (Posner, 1980). In this case, the eyes remain fixated and the 'spotlight' of attention is moved around independently of where one is looking. These 'covert' shifts of attention appear functionally similar to overt attention shifts, in that they allow the viewer to selectively process task-relevant information. However, the extent to which covert and overt attention rely on similar cognitive and neural mechanisms is controversial.

It is broadly agreed that the two systems are tightly coupled (Awh, Armstrong, & Moore, 2006; Corbetta et al., 1998; Smith & Schenk, 2012). For example, saccadic eye movements are preceded by a mandatory 'presaccadic' shift of attention (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995; Shepherd et al., 1986; Van der Stigchel and Theeuwes, 2005) and saccades suppress processing at non-target distractors location (Khan, Blohm, Pisella, & Munoz, 2015). Furthermore shifts of attention affect the trajectory of saccadic eye movements, consistent with the idea that shifts of attention activate a saccade plan (Sheliga, Riggio, & Rizzolatti, 1994; Van der Stigchel and Theeuwes, 2005). This association between saccade control and attention can also be observed at the neural level. Eye movements and covert shifts of attention appear to activate similar networks of brain areas, including the Frontal Eye Fields (FEF), the Lateral Intraparietal cortex and the Superior Colliculi (SC) (Andersen, 1989; Beauchamp, Petit, Ellmore, Ingeholm, & Haxby, 2001; Corbetta et al., 1998; de Haan, Morgan, & Rorden, 2008; Ignashchenkova, Dicke, Haarmeier, & Thier, 2004; Nobre, Gitelman, Dias, & Mesulam, 2000; Perry & Zeki, 2000), and lesions to these brain areas are associated with deficits of both covert orienting and saccade control Grosbras & Paus, 2002; Muggleton, Juan, Cowey, & Walsh, 2003; Müri, Hess, & Meienberg, 1991; Muri, Vermersch, Rivaud, Gaymard, & Pierrot-Deseilligny, 1996; Smith, Jackson, & Rorden, 2005, 2009a; Thickbroom, Stell, & Mastaglia, 1996). Moreover, electrical stimulation of FEF neurons in the non-human primate can elicit fixed-vector saccadic eye movements, and sub-threshold stimulation of the same neurons significantly enhanced perceptual discrimination at the saccade goal, even though the eyes were still centrally fixated (Moore, Armstrong, & Fallah, 2003; Moore & Fallah, 2001).

However there is less consensus about the precise nature of this coupling. One proposal, originally known as the Oculomotor Readiness Hypothesis (OMRH) (Klein, 1980a) and later as the Premotor Theory of Attention (Rizzolatti, Riggio, Dascola, & Umilta, 1987; Rizzolatti, Riggio, & Sheliga, 1994) holds that covert attention is entirely dependent on the oculomotor system, such that a covert shift of attention depends upon the activation of a saccade plan. Recently, Belopolsky and Theeuwes (2012) proposed a revision to Premotor theory, arguing that although saccade preparation is required for orienting of spatial attention, the maintenance of attention may not be associated with sustained activation of a saccade plan. In contrast, Schneider and Deubel have argued for an opposite direction of causation, proposing that attentional selection is a necessary precondition for the programming of accurate saccades (Schneider, 1995; Schneider & Deubel, 2002). Furthermore, Klein entirely rejected the idea of a causal link between saccade preparation and covert orienting,

based on the observation that preparing but cancelling a saccade does not elicit a shift of attention (Klein, 1980b; Klein & Pontefract, 1994a) (see also Born, Mottet, & Kerzel, 2014). Similar to Klein, our previous experiments have shown some behavioural and neuropsychological dissociations between covert attention and oculomotor control (Smith, Ball, & Ellison, 2014; Smith, Ball, Ellison, & Schenk, 2010; Smith, Rorden, & Jackson, 2004; Smith, Schenk, & Rorden, 2012). However, we proposed that the relationship between covert attention and oculomotor control depends on the mode of covert orienting being studied. Specifically, we have argued that exogenous attention (the rapid, unconscious but shortlived facilitation triggered by salient objects in the periphery) is tightly coupled to oculomotor control, whereas endogenous attention (the slow, volitional orienting to task-relevant locations) can be deployed independently of oculomotor control (Smith & Schenk, 2012).

The idea that exogenous covert orienting is more tightly coupled to oculomotor control than endogenous covert attention is consistent with a number of neuropsychological studies. Firstly, patients suffering from Progressive Supranuclear Palsy, a neurological disease characterised by destruction of the brainstem saccade centres which leads to paralysis of vertical gaze (Steele, Richardson, & Olszewski, 1964), experience impaired covert orienting along the vertical axis which is more severe for exogenous orienting than endogenous orienting (Rafal, Posner, Friedman, Inhoff, & Bernstein, 1988). Secondly, Smith et al. (2004) reported case of A.I who suffered from chronic ophthalmoplegia, a paralysis of the extraocular muscles which made her unable to make any eye movements. They observed a deficit of covert, exogenous attention with intact endogenous orienting. Similarly, Gabay, Henick and Gradstein (2010) demonstrated that patients with Duanes Syndrome (a developmental disorder associated with an inability to make abductive eyemovement) have impaired exogenous orienting but preserved endogenous orienting. Interestingly, Craighero, Carta, and Fadiga (2001), reported the case of eight patients with a chronic ophthalmoplegia caused by VIth nerve palsy that showed disrupted endogenous orienting, perhaps indicating that the decoupling of endogenous attention form oculomotor control may demand more time.

Consistent with the idea that attention could not be shifted to a location that cannot be reached with an eye-movement, Craighero, Nascimben, and Fadiga (2004) imposed an acute disruption of the oculomotor system by asking healthy participants to monocularly look at a screen rotated by 40° into the temporal hemifield. This manipulation is known to disrupt saccade programming (Boon, Theeuwes, & Belopolsky, 2017). Participants were presented with an informative foveal cue (a line on either the left or right of fixation) that accurately indicated the position of the upcoming target in 70% of the trials. The target could appear either in the nasal hemispace (i.e., at a position that can potentially be the goal of a saccadic eye-movement) or in the temporal hemispace (i.e., at a position that cannot become the goal of a saccadic eyemovement). As with the VIth nerve palsy patients, the attentional benefits of the valid cue was reduced when stimuli were presented in the temporal hemispace but not when presented in the nasal hemispace. The authors concluded that covert endogenous attention and saccadic eye movements share the same 'stop limit', which is the range of eye movements, also referred to Effective OculoMotor Range (EOMR) and is usually estimated to be around $+/-40^{\circ}$ (Guitton and Volle, 1987). However, using the same paradigm we observed a dissociation between saccade planning and endogenous covert attention (Smith et al., 2012). In our study eye-abduction led to an impairment of exogenous covert orienting to a peripheral cue, but did not affect endogenous attention directed by a central foveal cue. We speculated that this discrepancy in the results occurred because Craigheros' cue was lateralised to one or other side of fixation, and thus has a spatial component that may have engaged the oculomotor system. Consistent with this idea we showed that eye-abduction affected arrow cueing, but somewhat surprisingly, not gaze-cueing (Morgan, Ball, & Smith, 2014). Furthermore, when we applied eyeabduction during visual search we found that feature search in the temporal hemispace was disrupted, whereas inefficient, conjunction searches that rely on endogenous attentional processes are unaffected (Smith et al., 2010, 2014). Together, the neuropsychological and behavioural works seem consistent with the view that covert exogenous orienting of attention is dependent on the oculomotor system whereas covert endogenous orienting is largely independent of the oculomotor system.

An issue regarding the interpretation of both eye abduction paradigm and the patient studies is that in both cases there is abnormal eye-proprioception. Proprioception is essential for providing information about the initial motor location and is critical for controlling many aspects of upcoming planned movements (Paap & Ebenholtz, 1976). In order to execute an accurate eye movement, the eye-muscles communicate with the brain areas responsible for the oculomotor planning. In the case of eye-abduction, participants are asked to turn the eye by 40° into the temporal hemispace, thus the lateral rectus muscle is restricted and the medial rectus muscle tense, which leads to an abnormal proprioceptive signal. Eye proprioception is thought to play a role in spatial attention, for example Balslev, Newman, and Knox (2012) showed that extraocular muscles modulate the deployment of visual attention and Balslev, Gowen, and Miall (2011), using TMS, reported that eye proprioception influences the spatial distribution of attention resources. It has been proposed that the attention map incorporates eye-proprioception in order to align the retinotopic representations to the physical locations (Odoj & Balslev, 2016), suggesting that a distortion of proprioceptive signal would cause a systematic shift of the locus of attention. Thus, abnormal oculoproprioception, rather than disrupted saccade programming, could explain why the ability to orient attention is reduced in the case of eye-abduction and ophthalmoplegia.

One way to address this issue is to examine covert orienting to locations that can be seen, but are not directly accessible by a saccadic eye movement. The range of saccadic eye movements is very considerably smaller than the extent of the visual field. Indeed, the EOMR is estimated to be ~40° (Guitton and Volle, 1987), whereas the visual field extends to at least 90° in the temporal field (Niederhauser & Mojon, 2002). Here, we took advantage of this limitation on saccadic eye movements using an adaptation of the Posner cueing task where stimuli are presented in the far periphery but participant's eyes and trunk stay in their canonical, natural position. This manipulation allowed us to present stimuli beyond the range of eye movements without the potential confounds associated with eye-abduction. If exogenous but not endogenous orienting of attention is linked to the oculomotor system, covert, endogenous shift of attention should be unaffected by the eccentricity of the stimuli, whereas covert, exogenous orienting should be impaired when stimuli appear beyond the range of eye movements.

Three experiments were designed to test these predictions. Experiment 1 tested exogenous shift of attention whereas Experiment 2 tested endogenous shift of attention. Experiment 3 was designed to confirm the observations of Exp.1 and 2 using a within-participants design. In all three experiments the stimuli (placeholder and target) could appear at 2 different eccentricities (Below vs Beyond the EOMR) and at different stimulus-onset-asynchrony (SOAs). We used a Presentation in Extreme Periphery paradigm (PEP) as we presented stimuli at extremely unusual large eccentricities (up to 44°). Note that before starting each experiment we ran two blocks of trials in order to assess each participant's very own eye movement range, separately for nasal and temporal sides. This allowed us to calculate placeholders' eccentricities for each participant individually.

2. Establishing the effective oculomotor range

Each individual that took part in Experiment 1 (n = 25), Experiment 2 (n = 11) and Experiment 3 (n = 12) completed a simple goal directed saccade task in order to measure their effective oculomotor range (EOMR). Sample sizes for Experiments 1 & 2 were based on previous studies examining the effect of eye-abduction on covert attention (Craighero et al., 2004; Smith et al., 2012). The sample size for Experiment 3 was established using an apriori power calculation. This first task lasted about 30 min and was performed at least 24 h prior to the cueing task in order to allow the experimenter to analyse the data and create the images for the cueing task. During this first phase, participants were presented with a discrimination target that could appear at different angular positions on the horizontal axis, either to the left or to the right of fixation. The EOMR was calculated separately for nasal and temporal visual field, as the temporal field extended farther in the periphery compared to the nasal. Participants performed the task monocularly with the dominant eye, the non-dominant eye being patched (see Smith et al., 2014 for procedure regarding eye-dominance assessment).

2.1. Method

2.1.1. Apparatus

Eye movements of the dominant eye were recorded using a head-mounted EyeLink II (SR Research Ltd., Mississauga, Ontario) at a sample rate of 500 Hz. Because of the large range of eccentricities and the specifications of the eye-tracker, eyemovements were recorded in pupil only mode. Stimuli were generated using PsychoPy (Pierce, 2009) and saved as a jpeg. They were displayed on a 32 inches LED monitor (BenQ) driven by an NVIDIA GeForce GTX 750 Ti graphics board at a refresh rate of 60 Hz. The resolution of the monitor was set at 2560×1440 pixels, which corresponded to physical dimensions of 708 mm wide by 398 mm high. At a viewing distance of 30 cm, the display occupied a viewing area of 99° horizontally and 67° vertically.

2.1.2. Material and procedure

Each block of trials started after setting up the eye tracker and running a calibration phase. During calibration, five dots were presented successively on the screen, three dots on the horizontal axis [i.e., $(x_{dot1} = 1280 \text{ pixels}, y_{dot1} = 720 \text{ pixels})$, $(x_{dot2} = 905 \text{ pixels}, y_{dot2} = 720 \text{ pixels})$, $(x_{dot3} = 1655 \text{ pixels}, y_{dot3} = 720 \text{ pixels})$] and two dots on the vertical midline [$(x_{dot4} = 1280 \text{ pixels}, y_{dot4} = 470 \text{ pixels})$, $(x_{dot5} = 1280 \text{ pixels}, y_{dot5} = 970 \text{ pixels})$].

Participants were asked to fixate very precisely at each dot location, if fixations were correctly aligned with the calibration dots experiment was started. Otherwise a new calibration phase was initiated. As participants were asked to generate very large eye-movements, there was a risk of eye-tracking loss, it was thus important to have a correct calibration before starting the experimental blocks.

A drift correction was performed at the beginning of each trial; procedure is illustrated on Fig. 1. A fixation stimulus was initially displayed on the computer screen; this consisted of a fixation cross on a black background ($.20^{\circ} \times .20^{\circ}$). After a random time interval (400–1200 msec), the central cross was removed and the target was displayed (gap of 0 msec).

The target was a circle shape (diameter .20°) filled with black and grey gradient diagonal stripes orientated either leftward or rightward (see Fig. 1 for target illustration). The target was randomly presented at eight various possible eccentricities varying between 20° and 41° spaced by steps of 3°, to the right or the left of the fixation cross, with side kept constant within a block of trial. Participants were asked to fixate the target as quickly and as accurately as possible and perform an orientation discrimination task using a customized response box set with a TTL trigger. After a delay of two seconds, a new trial began. Session was divided in two blocks of 80 trials (10 repetitions per target eccentricity) and each was preceded by a 10 trials practice block.

2.2. Data selection, results and analyses

Amplitude of the initial saccade following target onset was considered for analysis, this corresponds to the difference between the initial and the final eye position. Each individual data set was analysed separately, however same exclusion criteria were used for all participants. Trials were rejected when (1) first saccade amplitude was of less than 2° (4.5% on average across participants), (2) a blink occurred before or after the saccade (1.1%), (3) the saccade was anticipatory (latency less than 80 msec; 6.4%), (4) initial saccade was in the opposite direction to the target or deviated too much from the horizontal axis (8.4%) and (5) the average eye-position before the saccade deviated from the fixation cross by more than 1° in the horizontal direction (14.6%).

Analyses were achieved using R 3.0.3 (R Core Team, 2014), data visualisation was performed with the package ggplot2 (Wickham, 2009).

2.2.1. Establishing the effective oculomotor range (EOMR) Data were filtered to removed saccades with amplitude less than 75% of the target eccentricity and saccades with an



Fig. 1 — Sequence of events in the EOMR establishment task. Each trial started with a drift correction, followed by a central fixation cross. Target was always presented on the horizontal meridian and participants were instructed fixate as accurately as possible the target and make an orientation discrimination response.

amplitude greater than 25% of the target eccentricity. The EMOR was defined as the point at which the mean saccadic gain, defined as the ratio of the actual saccade amplitude to the target eccentricity, dropped to .8 or below. The participants mean saccade amplitude for targets at this position plus 2 standard deviations was used to set the target position in the Beyond condition. Their mean saccade amplitude minus 2 SD in the 20° condition was used to set the target position in the Below condition. Distribution of all participants' saccade amplitude for each target eccentricities are shown on Fig. 2 and the mean amplitudes are reported in Table 1.

We also looked at the frequency of corrective saccades, which are saccades that are likely to happen after an inaccurate primary saccade. After selection criteria (see Data selection) and across all our participants, 25% of the initial saccades were followed by a corrective saccade in the same direction as the target. Corrective saccades were mostly present when target was presented at large eccentricities, as 32% of the saccades made to a target presented a 41° were followed by a corrective saccade and their mean amplitude for each target eccentricity are shown on Fig. 3.

3. Experiment 1 – covert, exogenous orienting

3.1. Method

3.1.1. Participants

Twenty five volunteers, between 18 and 28 years old ($M_{age} = 19$ years, 20 females); took part in Experiment 1. Participants reported having normal vision and were all unaware of the purpose of the experiment. Written informed consent was gathered for all individuals and they received course credit for participating. Studies were approved by the Department of Psychology Research Ethics Committee and were conducted in accordance with the BPS code of ethics. One participant showed more than 40% of error rates and was excluded. Another participant failed to maintain fixation so did not complete the data collection.

3.1.2. Materials and procedure

3.1.2.1. STIMULI. The initial array comprised a fixation point ("+" sign, .20°) and two white placeholders (1 pixel thick, .50° square contours) on a black background (<.10 cd/m²). The cue was the appearance of a second contour with a thickness of 2 pixels around one of the two placeholders. The target was a circle shape (.20°) filled with black and grey gradient diagonal stripes (see Fig. 4 for example).

In order to equate proximal (Below EOMR) and distal (Beyond EOMR) placeholders and target sizes were scaled in accordance with the cortical magnification equation of Rovamo and Virsu (1979). Both nasal (*n*) and temporal (t) placeholder sizes were scaled according to the following two formulas,

$$n = p^* [(1 + .33^* e) + (.00007^* e^3)]$$
 (1)

$$t = p^* \left[(1 + .29^* e) + (.000012^* e^3) \right]$$
(2)

where *p* was the placeholder size and *e* was the placeholder eccentricity. Placeholder/cue eccentricities ranged between 10° and 20° for the Below EOMR condition and between 30 and 44°¹ for the Beyond EOMR condition. For example, a cue of .50° will have a size of $2 \times 2^{\circ}$ when presented at 10° and a size of $6.5 \times 6.5^{\circ}$ when presented at 30°.

3.1.2.2. PERIPHERAL CUEING TASK. Each trial began with the presentation of a fixation point and placeholders for 1000 msec. The cue then appeared at one of the peripheral locations for 100 msec. After a further delay of 0, 100, 200 or 500 msec, the target appeared, this produced SOAs of 100, 200, 400 or 600 msec. The target remained visible until the manual response was made.

On "Valid" trials, the target appeared at the previously cued location (2/5 of trials) whereas on Invalid trials, the target appeared contralateral to the cued location (2/5 of trials). Valid and Invalid trials were interleaved with catch trials, where the cue appeared but without any target (1/5 of the total trials). Reaction Times (RTs) were measured using a button box set with a TTL trigger, participants were asked to press the upper button when they detected a target being present in one of the two placeholders and lower button when target was absent (catch trials). Participants were instructed to maintain fixation, not to make any eye movements and to respond as fast as possible upon target detection. After button response, a black screen was presented for 2000 msec, before the next trial to begin. Experimental procedure is presented on Fig. 4.

All the different conditions were manipulated within each block of trial, 20 repetitions per valid/invalid condition and 10 repetitions for catch trials were assessed. This led to a total of 800 trials divided into ten blocks of 80 trials.

3.1.2.3. DATA SELECTION AND ANALYSES. Before analysing data, trials were filtered and excluded if participants made a detectable saccadic eye movement (i.e., amplitude of more than 2°) which corresponds to 11.3% of the observations. Trials with response time of less than 100 msec were excluded as they were considered as anticipations (4.5%) and outliers that were more than 2.5 standard deviation greater than the individual's mean reaction time were removed (2.2%). Catch trials were not analysed for our purpose and incorrect responses (i.e., participants wrongly detected the presence/ absence of the target) were discarded (.49%). Altogether these criteria resulted in a total of 12.5% of trials rejected, leading on average to 592 experimental trials per participant.

Mean manual response times (RTs) were calculated for each participant and were then averaged across participants. Previous studies using eye-abduction paradigm did not report any significant difference between nasal and temporal directions when participant's eyes were in their canonical

¹ Note that the eccentricity of 20° was used as a default value when participants indicated that they were not able to fully see the placeholder/target because it accidentally fell into their blindspot. Due to the display restriction, 44° was the maximal eccentricity at which we could present the cue/target. We used it as a default value for four participants for whom the mean+2sd was larger than this maximum.



Fig. 2 – Distributions of first saccade amplitude (in degrees of visual angle) for Nasal (grey) and Temporal (black) target side of presentation, separately for each target eccentricity for all individuals. Black dotted line represents the actual target position. Amplitudes were grouped into 1° bins.

Table 1 – Mean saccade amplitude (in degrees of visual angle), and standard errors (in parentheses) as a function of target eccentricity $(20-41^{\circ})$.

		Target eccentricity (degrees)								
	20	23	26	29	32	35	38	41		
Mean Amplitude of the 1st Saccade (degrees)	18.9	21.1	23.2	24.8	26.3	27.1	28.5	29.3		
(Standard Error)	(.07)	(.1)	(.14)	(.13)	(.14)	(.15)	(.16)	(.18)		



Fig. 3 – Frequency of corrective saccades (grey bars) and mean amplitude (black line) as a function of target eccentricities. Note that for target eccentricities of 35° or greater the first corrective saccade was not sufficiently large to foveate the target.

position (Craighero et al., 2004; Smith et al., 2012, 2014), hence data were collapsed across both directions for analysis. Note that Rafal, Henik, and Smith (1991) did observe a nasotemporal asymmetry in using a peripheral cueing task, but their task required a manual localisation which confounded the effects of covert attention with stimulus-response compatibility effects.

Repeated measure ANOVA tested the RTs with placeholder eccentricity (Below or Beyond), validity (valid or invalid) and SOAs (100, 200, 400 or 600 msec) as factors. In case of a violation of the assumption of sphericity (Mauchly's test of sphericity), we used the Greenhouse-Geisser correction to report the corrected degrees of freedom and p values. Significant effects were explored using Bonferroni corrected paired sample t-tests, where the p value was multiplied by the number of comparison. Statistical analyses were performed using R 3.0.3 (R Core Team, 2014), anovas were conducted using the ez package (Lawrence, 2011), and data visualisation was performed with the package ggplot2.

3.2. Results & discussion

3.2.1. Initial fixation positon

To ensure that each participant was presented with the placeholder at the accurate eccentricity, it was important that they were correctly positioned at the centre of the screen at the beginning of each trial. We thus checked the position of the initial fixation relative to the fixation cross. Eyes were mostly perfectly aligned with the centre of the screen, mean deviation from the fixation cross remained very small, that is $.14^{\circ}$ (range: $-2.33^{\circ} - 2.66^{\circ}$).

3.2.2. Manual reaction time

Repeated measure ANOVA revealed a main effect of cue eccentricity (F(1,22) = 24.71, p < .001, $\eta^2_{\ p} = .52$), with participants being on average longer in the Beyond (521 msec) compared to the Below (503 msec) condition. Cue validity did not show any main effect (F(1,22) = 1.33), however the interaction between eccentricity and validity was significant (F(1,22) = 6.69, p = .02,

 η^2_p = .23). Pairwise t-tests showed that the difference in mean RT observed between Valid and Invalid condition was only significant for Below EOMR condition (Invalid Below = 508 msec, SD = 153, Valid Below = 498 msec, SD = 160, t(22) = 2.15, Bonferroni corrected p = .025, Invalid Beyond = 520 msec, SD = 154, Valid Beyond = 523 msec, SD = 160, t(22) = .66).

As can be seen on Fig. 5 mean RT varied with SOA (F(2.56,56.4) = 15.99, p < .001, $\varepsilon = .78$, $\eta^2_p = .42$), being gradually shorter as the SOA increased, until 600 msec where it increased slightly again. The t-test revealed that each SOA condition only differed significantly from the 100 msec condition (SOA 100: 532 msec, SD = 154, SOA 200 = 508 msec, SD = 156, t(22) = 5.87, SOA 300 = 498 msec, SD = 153, t(22) = 9.38, SOA 600 = 510 msec, SD = 150, t(22) = 3.34, Bonferonni corrected *P* values always <.001), indicating that the mean RTs were systematically longer for the shorter SOA condition. We did not observe any significant interaction between SOA and our two other factors (all Fs< = 1.4).

3.2.3. Accuracy

When participants correctly detected the presence or absence of a target the trial was considered as correct whereas trial was incorrect when they responded that the target was absent while present. Here, accuracy refers to the percentage of correct responses. Across all participants accuracy was of 98.7% (range: 95.77% - 99.88%). As accuracy was very high, we will just report the means for each condition separately. As shown on Table 2, participants were less accurate in the 600 msec SOA condition compared to the three other ones. This simply might be due to participant's expectation: as the SOA was very long, they wrongly expected the absence of target, leading them to make an incorrect response. The mean reaction time for incorrect responses in the 600 msec SOA condition was 315 msec, which indicates that incorrect responses were indeed due to anticipation. Accuracy did not vary with stimuli eccentricity; hence participants correctly detected target presence even if it was presented in the far periphery.

3.3. Discussion

In line with previous reports the present experiment showed that stimuli presented outside the usual range of saccadic eyemovements produce a deficit of exogenous/reflexive attention. Furthermore, it revealed that using a more natural set up, like a Presentation in Extreme Periphery (PEP) paradigm, produced a similar deficit as the eye-abduction paradigm, suggesting that this effect results from the limitations linked to the oculomotor plan rather than any other motor constraints.

We did not observe an Inhibition of Return (IOR) either in the Below or in the Beyond condition, although there was a hint of an IOR in the 600 msec SOA in the Beyond condition. This result was a bit surprising, given that our previous work has found normal IOR effects beyond the EOMR (Smith, Jackson & Rorden, 2009, Smith et al., 2004 although see Michalczyk, Paszulewicz, Bielas, & Wolski, 2018 for a contrary view) and Bao and colleagues report that IOR effects get larger with increasing stimulus eccentricity (Bao, Lei, et al., 2013; Bao & Pöppel, 2007; Bao, Wang, et al., 2013). One possibility is that the lack of IOR reflects the difficulty of the task. IOR is known





to be highly sensitive to task difficulty, such that the onset of IOR is delayed as task difficulty increases (Lupiáñez, Milliken, Solano, Weaver, & Tipper, 2001). The manual RTs we observed were quite long for a detection task (~500 msec), and it may be that target detection in the far periphery is sufficiently difficult to push the onset of IOR back beyond the 600 msec SOA we measured here.

These data demonstrate that covert, exogenous shifts of attention are restricted to the effective oculomotor range, consistent with previous evidence of a tight coupling between exogenous attention and the oculomotor system. Experiment 2 was designed to test the hypothesis that covert, endogenous orienting can be decoupled from oculomotor control, and therefore should not be restricted to the effective oculomotor range. To this end, we used the same methodology as proposed by Craighero et al. (2004) but with a PEP paradigm instead of eye-abduction.

4. Experiment 2: Endogenous covert orienting

4.1. Method

4.1.1. Participants

Eleven volunteers, between 19 and 35 years old ($M_{age} = 21$ years, all female) took part in Experiment 2. Participants reported having normal vision and were all unaware of the



Fig. 5 – Mean manual reaction time (RT) in ms as a function of Stimulus Onset Asynchrony (SOA) and cue validity for Below and Beyond the EOMR separately. Error bars represent +/- 1 standard error.

Table 2 — Mean detection accuracy in percentage as a function of SOA, Eccentricity and Cue validity.

		_	SOA (ms)					
		100	200	300	600			
Below EOMR	Valid	99.4	99.7	99.2	96.5			
	Invalid	99.8	99.6	99.6	97.4			
Beyond EOMR	Valid	99.4	98.9	99.1	95.9			
	Invalid	99.8	99.7	98.8	96.1			

purpose of the experiment. Written informed consents were gathered for all individuals and they received course credit for participating.

4.1.2. Materials and procedure

Each trial began with the presentation of a fixation square $(.20^{\circ})$ and two placeholders (1 pixel thick .50° squares) on a black background for 1000 msec. After this delay predictive cues were presented which consisted of a thin line attached to the fixation box (.40°) for 300 msec. After cue appearance the initial fixation screen was presented for 300 or 600 msec (SOA of 600 or 900 msec). After this delay, the target, a circle filled with black and grey lines was presented and remained visible until manual response was made (see Fig. 6 for experimental set up). In the target present experimental trials, the target could appear at a previously cued position in 3/4 of the trials ("valid" trials), and in 1/4 of the trials it could appear at the opposite position ("invalid" trials). Valid and invalid trials were filled with catch/no target trials. As in Experiment 1, participants were instructed to maintain fixation, not to make any eye movements. They were told to respond as fast as possible to the target by pressing a button on a response box set up with a TTL trigger and were not informed about cue predictability before the study began. This was followed by the presentation of a black screen for 2000 msec, after this delay the next trial began. All the different conditions were manipulated within each block of trial, there were a total of 480 repetitions for valid, 160 repetitions for invalid condition and 80 repetitions for catch trials. This led to a total of 720 trials divided into ten blocks of 72 trials. The order of the

conditions was randomized in each block. A short practice block of 20 trials preceded each session.

Placeholders eccentricities were calculated based on to each individual's EOMR and sizes were scaled according to the cortical magnification factor (see Experiment 1).

4.1.3. Data selection and analyses

We applied same criteria as in Experiment 1. Saccadic eye movement selection (i.e., amplitude $>2^{\circ}$) led to 4.7% of rejection, short (<100 msec) and long RT (>2.5 SD) led to .1% and 2.8% of rejection respectively and catch trials as well as incorrect responses (1.1%) were also discarded. This resulted in a total of 16% of trials rejected leading on average to 515 trials per participant. For data analyses and software used, see Data selection and analyses section of Experiment 1.

4.2. Results & discussion

4.2.1. Initial fixation positon

As for Experiment 1, we looked at participant's eye position on the fixation square. Participants were on average perfectly aligned with the central square, eye position variation ranged between -1.98 and 1.97° ($M_{\rm fix} = -.02^{\circ}$).

4.2.2. Manual reaction time

Results of mean RTs across all participants are resumed on Fig. 7. On average participants were longer to respond in the Invalid condition (448 msec) compared to the valid condition (401 msec), repeated measure ANOVA revealing a significant effect of cue validity $[F(1,10) = 61.69, p < .001, \eta^2_p = .86]$. As with Experiment 1 there was a small but significant effect of placeholders eccentricity on mean reaction time $[F(1,10) = 5.42, p = .04, \eta^2_p = .35]$ as participants were on average longer in the Beyond compared to the Below condition (419 msec and 406 msec respectively). RT did not vary according to SOA, but we did find an interaction between SOA and cue eccentricity $[F(1,10) = 6.59, p = .02, \eta^2_{p} = .39]$, such that RTs tended to be faster in the Below compared to the Beyond condition at the 600 msec SOA [396 msec, SD = 88 and 412 msec, SD = 97 respectively for Below and Beyond; $t_{(10)}=$ 3.05, Bonferonni corrected P < .05], but not at the 900 msec SOA [416 msec, SD = 94 and 426 msec, SD = 94 respectively for Below and Beyond, $t_{(10)} = 1.92$, Bonferonni corrected P = .082].

The difference between invalid and valid cues for both cues eccentricities was calculated, revealing that on average invalid cues delayed response time by 50 msec in the Below and 45 msec in the Beyond condition. This difference was not statistically significant [F(1,11) = 1.11].

4.2.3. Accuracy

Accuracy was on average very good (98.9%) and did not vary according to either cue eccentricity, validity or SOA.

4.3. Discussion

Experiment 2 was designed to disentangle between the conflicting results previously reported in the literature regarding the link between endogenous cueing and the oculomotor programming. Consistent with the hypothesis that



Fig. 6 – Sequence of events in the endogenous/central cueing condition when placeholders were presented Below (a) or Beyond (b) the EOMR.



Fig. 7 – Mean manual reaction time (RT) in ms as a function of Stimulus Onset Asynchrony (SOA) and cue validity for Below and Beyond the EOMR separately for the endogenous cueing task. Error bars represent +/- 1 standard error.

endogenous attention can be decoupled from oculomotor control, there was no interaction between cue validity and placeholder eccentricity, suggesting that covert, endogenous orienting of attention was not disrupted when stimuli were presented outside the participants' effective oculomotor range. Altogether, these results are accordance with previous studies reporting that motor programming of a saccadic eye movement is neither necessary nor sufficient to trigger a voluntary shift of attention (Hunt & Kingstone, 2003; Klein, 1980b; Klein & Pontefract, 1994b; Smith et al., 2012).

5. Experiment 3: Endogenous and exogenous covert orienting

The results of Experiment 1 showed that exogenous covert orienting is limited to the range of eye-movements and the results of Experiment 2 suggested that endogenous covert orienting is not. It is tempting to interpret these results as a replication of the dissociation between impaired exogenous orienting and intact endogenous orienting previously reported in ophthalmoplegic patients. However, comparisons between Experiments 1 and 2 should be made with caution for several reasons. Firstly, the SOAs used in the two experiments were very different and it is well established that attentional effects are highly sensitive to SOA. Secondly the sample sizes were also rather different. Finally, in Experiment 1 the attentional cue appeared in the periphery, whereas in Experiment 2 the cue was central and therefore potentially much easier to detect. It is therefore possible that participants simply failed to detect the cue in Experiment 1. To address these issues we conducted a third experiment in which we examined endogenous and exogenous covert orienting within and beyond the range of eye-movements using the same SOAs in the same participants. Participants also completed an additional task in which they simply reported the location of the exogenous cue, which allowed us to rule out the possibility that participants were unable to detect it. Prior to beginning the experiment we conducted two apriori power analyses using the package pwr (Champely, 2012) to establish the minimum sample sizes required to observe an endogenous cueing effect in the Below and Beyond condition, based on the data from Experiment 2. The analysis estimated that at least 5 participants would be needed to obtain a statistical power at the recommended .80 level (Cohen, 1988) in the Below condition ($M_{diff} = 45$ msec, $sd_{diff} = 23.17$, $d_z = 1.94$) and a minimum of 10 participants would be required for the Beyond condition ($M_{diff} = 47$ msec, $sd_{diff} = 36.03$, $d_z = 1.32$).

5.1. Method

5.1.1. Participants

Twelve volunteers, between 19 and 44 years old ($M_{age} = 31$ years, seven female) took part in Experiment 3. Participants reported having normal vision and were all unaware of the purpose of the experiment.

5.1.2. Materials and procedure

Materials and Procedure for Experiment 3 were the same as for Experiment 1 (Exogenous) and Experiment 2 (Endogenous) (see Figs. 4 and 6) with the exception that the SOAs were set to 200 and 400 msec for both tasks. All the different conditions were manipulated within each block of trials and the order of the conditions was randomized. Endogenous and Exogenous tasks were run separately. For the Exogenous task, there was a total of 264 trials divided into 3 blocks of 88 trials (120 repetitions for valid, 120 repetitions for invalid condition and 24 repetitions for catch trials). Before starting the Exogenous task, we made sure that participants were able to detect the exogenous cue when presented in the Beyond condition. To this end participants completed 20 trials in which they reported the location of a cue which could be flashed either to the left or to the right of fixation. All participants were 100% accurate, which confirmed that they were perceptually able to detect the peripheral cue. For the Endogenous task, 528 trials were presented divided into 6 blocks of 88 trials (360 repetitions for valid, 120 repetitions for invalid and 48 for catch trials). A short practice block of 20 trials preceded each session. Participants were not informed about cue predictability before the experiment began. As for Experiment 1 and 2, placeholders eccentricities were calculated based on each individual's EOMR and sizes were scaled according to the cortical magnification factor (see Experiment 1).

5.1.3. Data selection and analyses

We applied same criteria as in Experiment 1 and 2. Saccadic eye movement selection (i.e., amplitude $>2^{\circ}$) led to 3.7% of rejection, short (<100 msec) and long RT (>2.5 SD) led to .6% and 2.4% of rejection respectively and catch trials as well as incorrect responses (3.9%) were also discarded. In total 16.7% of trials were excluded. For data analyses and software used, see Data selection and analyses section of Experiment 1.

5.2. Results & discussion

As for Experiment 1 and 2, participants eye-position at the beginning of each trial was aligned with fixation, deviation was on average of $.05^{\circ}$ (range between- 2.09° and 2.49°).

5.2.1. Manual reaction time

Correct responses to target present trials were analysed and mean reaction times were subjected to a 2*2*2*2 mixed model ANOVA with within subject factors of task (Endogenous vs Exogenous), cue validity (Valid vs Invalid), eccentricity (Below vs Beyond) and SOA (200 vs 400 msec). The ANOVA revealed a main effect of cue validity, participants being on average longer in the Invalid (493 msec) compared to the Valid (425 msec) condition [F(1,11) = 29.22, p < .001, $\eta_p^2 = .72$]. We also observed a significant 2-way interaction between cue validity and cue eccentricity [F(1,11) = 5.51, p < .05, $\eta_p^2 = .33$] and a significant 2-way interaction between task and cue validity [F(1,11) = 10.39, p < .001, $\eta_p^2 = .48$].

ANOVA also revealed a significant 3-way interaction between cue validity, eccentricity and task [F(1,11) = 23.66,p < .001, $\eta_p^2 = .68$]. This interaction was broken down into a 2 (eccentricity) by 2 (cue validity) repeated measure ANOVA at each level of task. For the Exogenous cueing task, cue validity interacted with cue eccentricity [F(1,11) = 15.06, p < .01, $\eta_p^2 = .58$]. Bonferroni corrected pairwise t-tests showed that the difference in mean RT between Valid and Invalid condition was only significant when cue/target were presented Below the EOMR [Invalid Below = 472 msec, SD = 146, Valid Below = 418 msec, SD = 121, t(11) = 7.27, p < .001, Invalid Beyond = 474 msec, SD = 152, Valid Beyond = 473 msec, SD = 169, t(11) = .06]. In contrast, for Endogenous task, the ANOVA revealed a main effect of validity [F(1,11) = 19.63, $p < .001, \eta_p^2 = .86$], but no effect of eccentricity and no interaction (all Fs \leq 2.07). As can be seen on Fig. 8, this 3-way interaction was driven by a cueing effect present for both Below and Beyond EOMR condition in the Endogenous task, but only in the Beyond EOMR condition in the Exogenous task.

Finally, a 3-way interaction between SOA, cue validity and task was observed [F(1,11) = 8.54, p < .05, $\eta_p^2 = .43$]. Inspection of Fig. 8 showed that in the Exogenous task, the validity effect varied with SOA, the difference between Valid and Invalid trials being greater for SOA of 200 msec compared to 400 msec, the interaction was marginally significant [F(1,11) = 5.13,



Fig. 8 – Mean manual reaction time (RT) in ms as a function of Stimulus Onset Asynchrony (SOA) and cue validity for Below and Beyond the EOMR separately for the endogenous and exogenous cueing task. Error bars represent +/- 1 standard error.

p = .04, $\eta_p^2 = .31$]. However in the Endogenous task, SOA did not significantly affect mean RTs [F(1,11) = 2.50] and did not interact with the other factors (all Fs \leq 4.01).

5.2.2. Accuracy

Accuracy was on average very good (96.15%) and did not vary according to the task (Endogenous = 96.03%, Exogenous = 96.33%). None of the different factors (Eccentricity, validity or SOA) had any effect on accuracy.

5.2.3. Discussion

Experiment 3 was designed to directly compare the effect of exogenous and endogenous shift of attention within participants and using the same SOAs for both tasks. Results are in accordance with the observation reported in Exp.1 and Exp.2; that is, we observed a strong cueing effect when participants are asked to endogenously shift their attention irrespective of whether stimuli are presented within or beyond the range of eye movement. On the other hand, when attention was summoned exogenously we observed a cueing effect solely when cue/target were presented within the range of eye movement. When stimuli were presented outside the range of eye-movement the cueing effect was almost completely abolished.

6. General discussion

The goal of the present work was to test the claim that exogenous but not endogenous covert attention is mediated by the oculomotor system (Smith et al., 2014; Smith & Schenk, 2012). More specifically we tested whether cue presented outside the range of eye movement disrupted exogenous but not endogenous covert orienting. In Experiment 1 there was no exogenous covert orienting when stimuli were presented beyond the participant's usual range of eye movement (EOMR), but we did observe an effect when presented within this range. These results are in accordance with previously reported studies with patients (Gabay, Henik, & Gradstein, 2010; Rafal et al., 1988; Smith et al., 2004) and with the eye-abduction paradigm (Smith et al., 2010, 2012, 2014). In contrast, Experiment 2 demonstrated that the endogenous shift of attention was unaffected when stimuli appeared beyond the EOMR. Finally, Experiment 3 confirmed the dissociation using a within participant design and the same timing for both Endogenous and Exogenous cueing. Together these data are consistent with the proposal that covert, endogenous orienting can be decoupled from oculomotor system, whereas covert exogenous orienting cannot.

Our findings appear contrary to the findings of Craighero et al. (2004, 2001), who observed, in an endogenous cueing task, that the attentional benefit for valid cues was reduced when stimuli were presented at a location not reachable by a saccadic eye-movement. The precise reason for the inconsistency between Craighero's results and the current data is not clear. We have previously argued that the central cue used by Craighero et al. is both spatial and predictive, and thus the cueing effect they observed may reflect elements of both exogenous and endogenous attention (Smith et al., 2012). We speculated that eye-abduction affected the exogenous contribution of the cueing effect, thus reducing the overall effect. Consistent with this explanation, covert orienting to a nonspatial, predictive central cue that engaged purely endogenous attention was not affected by eye-abduction (Smith et al., 2012) whereas orienting to a nonpredictive spatial cue that engaged reflexive attention (an arrow) was affected by eye abduction (Morgan et al., 2014). On first inspection this explanation cannot easily account for the current data, as the central cue condition in Experiment 2 was similar to that used by Craighero et al. (2004). However, the predictive power of the cues was different in the two studies. Our cue predicted target location on 75% of trials, whereas Craigheros cue predicted target location on 66% of trials. It may be that the greater predictive power of our cue engaged the endogenous orienting system, whereas the cueing protocol used by Craighero et al., engaged both exogenous and endogenous mechanisms.

A close reading of Craighero et al. (2004) suggests a less theoretically interesting possibility, in that they do not actually report a significant interaction between Validity, Hemifield and Eye Position. Rather, their conclusion that eyeabduction disrupts endogenous orienting is based on observing a significant cueing effect in the Eye Abducted/ Nasal Hemifield condition, but no significant cueing effect in the Eye Abducted/Temporal Hemifield condition. It is therefore possible that their failure to observe a cueing effect in the temporal hemispace during eye-abduction is a type II error rather than a genuine disruption of endogenous orienting.

The conclusion that endogenous orienting is dissociable from oculomotor control echoes that drawn by Belopolsky and Theeuwes (2009, 2012), who showed that participants could sustain attention at a location while simultaneously supressing saccade programming to that same location. In these experiments both exogenous and endogenous covert orienting were associated with the activation of a saccade motor plan. However, in the case of endogenous attention the saccade execution was rapidly suppressed without disrupting the allocation of attention. Belopolsky & Theeuwes proposed a revision to Premotor Theory that they called a 'Shifting and Maintenance (S&M) account of attention'. This revised theory retains the core assumption of Premotor Theory, that endogenous orienting depends upon a saccade motor plan but argues that once attention has moved; an active saccade plan is not required to sustain attention. Our data suggest that this revised S&M assumption needs to be updated to account for the finding that endogenous orienting of attention can occur in the absence of a saccade plan. Indeed, it is worth noting that, while Belopolsky & Theeuwes elegantly demonstrated a dissociation between endogenous attention and saccade programming, they do not demonstrate a causal link between saccade programming and attention shift. This is an important issue, because the 'mandatory coupling' between covert orienting and saccade motor control might occur because attending a location leads to saccade programming, which is the opposite of what Premotor Theory of Attention predicts (see Deubel & Schneider, 1996; Schneider, 1995).

One can also interpret our results in terms of Premotor theory. The theory argues that covert attention is driven by activation in 'spatial pragmatic maps', which are the brain areas used to encode the targets of goal directed actions. In the case of stimulus driven eye-movements these spatial pragmatic maps are probably represented in the superior colliculus (SC). In this view, the probability of observing a reflexive shift of attention to any given spatial location depends primarily on the level of activity in the SC associated with the location of the peripheral cue. At large eccentricities we know that stimulus driven saccades systematically undershoot the intended goal (Frost & Pöppel, 1976; Stahl, 1999), and this undershoot reflects the locus of activation in the SC (Vitu, Casteau, Adeli, Zelinsky, & Castet, 2017) rather than visuomotor strategy designed to minimize accidental overshoot (Deubel, Wolf, & Hauske, 1986; Henson, 1978; Robinson, 1973). In the case of exogenous attention the peripheral cue generates a peak of activity in the SC. When the cue appears beyond the EOMR this peak will be closer to fixation than the actual location of the cue. As a consequence, the shift of attention should also be shifted towards fixation, and not at the actual spatial location of the cue. Thus, according to Premotor Theory, peripheral cues beyond the EOMR should elicit a shift of attention to the edge of the EOMR, not the actual spatial location of the cue. Consistent with this view, there is some evidence that saccade adaptation can result in reflexive shifts of attention that are directed to the adapted saccade goal, rather than the veridical location of the cue (Collins & Dore-Mazars, 2006). In contrast, Endogenous shifts of attention generated by centrally presented cues rely on activation of spatial maps in the Frontal Eye Fields (Smith et al., 2005; Smith, Jackson, & Rorden, 2009b; Taylor, Nobre, & Rushworth, 2007) and attention related activation in FEF is dissociable from saccade related activation (Juan et al., 2008; Juan, Shorter-Jacobi, & Schall, 2004; Sato & Schall, 2003; Thompson, Biscoe, & Sato, 2005). This dissociation between oculomotor and visual selection means that the location of activation peaks in FEF accurately signals the cued location. As a consequence, Endogenous covert attention may be unconstrained by the EOMR. Our data could therefore be considered as consistent with the weak version of Premotor theory proposed by Smith and Schenk (2012), in which only exogenous shifts of attention rely on saccade programming.

However, these data may be understood in terms of a Biased Competition approach to attention, in which activation in the motor system influences competitive interactions in the visual system (Desimone, 1998). In this model, signals relating to stimulus salience (e.g., their brightness, size, contrast, orientation) compete with each other in a topographic map of space, called a priority map (Bisley & Goldberg, 2010), in a winner-takes-all competition. This competition is biased by the current goals of the observer, such as the knowledge that a target is likely to appear at particular location, which allows the observer to bias the outcome of the competition towards task-relevant locations. The signal that wins the competition can be used by the visual system to prioritize processing and/ or by the oculomotor system to specify the goal of a saccade eye movement. The oculomotor signals are self-reinforcing; such that activation in the oculomotor system is fed back into the salience map, thus further biasing activity in favour of the activated location (Bisley, Mirpour, Arcizet, & Ong, 2011). This interaction will typically produce very rapid selection of a peripherally cued location, which will facilitate target detection. However, when the cued location is beyond the EOMR there will be a discrepancy between the representation of the cue location in the SC (which is biased towards fixation: Vitu et al., 2017) and the representation of the cue location in the rest of the visual system which is veridical. This mismatch will lead to a competition between the representation of the cued location in the visual system and its representation on the SC map. This competition takes time to resolve, and may end up with selection of the location represented in the oculomotor system rather than the location of the target, thereby impeding target detection. We can therefore understand the failure of exogenous orienting to cues beyond the EOMR as the consequence competition between different sources of input to the priority map.

We have shown that exogenous orienting is abolished when a location is beyond the range of saccadic eye movements. However, several studies have argued that exogenous attention is independent of the oculomotor system. For example, MacLean, Klein, and Hilchey (2015) adapted the dual task procedure of Klein & Pontefract (1994), and reported that exogenous orienting does not facilitate saccadic reaction times. In a related study Dunne, Ellison, and Smith (2015) have shown that instrumental conditioning of the eye-movement system modulates saccade latencies, but has no effect on exogenous covert orienting. On first inspection these studies seem hard to reconcile with the proposal that exogenous attention relies on saccade programming. However, we believe these studies need to be interpreted with caution. MacLean et al. (2015) used an SOA of 250 msec, allowing ample time for suppression of saccade programming following a shift of attention. Indeed, the authors themselves concede that their data only demonstrates that maintenance, not orienting of attention can be decoupled from programming of a saccade, as suggested by Belopolsky and Theeuwes (2009, 2012). Furthermore, MacLean study utilises very high proportion of 'no-go' trials, where a cue appears but no saccade is permitted. This design is problematic, because the presence of a high proportion no-go trials can mask saccadic priming effects caused by peripheral cues (Belopolsky & Theeuwes, 2012; Smith & Casteau, 2018). The finding that oculomotor learning doesn't modulate the magnitude of cueing effects (Dunne et al., 2015) is interesting, but one might predict that rewards that facilitate saccadic reaction time should modulate the speed at which exogenous attention shifts to the cued location, rather than the amount of attention allocated to the cued location. Dunne et al., sampled attention at a single timepoint, so it remains possible that instrumental conditioning of saccades changed in the time-course of attention. Thus, in our view, neither of these studies unambiguously demonstrates a dissociation between exogenous, covert orienting and oculomotor control.

Our finding of impaired exogenous orienting beyond the range of eye-movements may also be relevant to understand the 'attentional window', which describes a form of spatial attentional control that sets a limit on the range of locations from which salient items can summon attention (Belopolsky & Theeuwes, 2010; Belopolsky, Zwaan, Theeuwes, & Kramer, 2007). The size of the attentional window can be voluntarily modulated with a maximum size of 29.74 +/- 1.82° for young adults (Hüttermann, Bock, & Memmert, 2012). This figure roughly corresponds to the average of the 1st saccade amplitude we observed for our most eccentric target positions, and may suggest that the maximal range of eye-movement sets an upper limit on the size of the attentional window.

It might be argued that there are some limitations to our measure of the EOMR. First, we have decided to take into account the amplitude of the very first saccade. However, it is very well known that there is a large discrepancy between the actual saccade landing position, at the level of saccade execution, and the saccade goal, that is a the level of the saccade plan. Saccades are known to undershoot the target position by about 10% of its eccentricity, and as the target is presented further in the periphery the likelihood of producing a corrective saccade is increased (Becker & Fuchs, 1969). The most common explanation for this saccadic undershoot is that it reflects visuo-motor strategies. If this was correct, taking only the first saccade as a measure of participants' range of eye-movement would give an inaccurate estimate of the saccade goal that would reflect a visuo-motor strategic saccade execution. However, empirical tests of the 'visuomotor' explanation are more consistent with the idea that the undershoot observed during large saccades is likely to originate at (or upstream of) the SC, suggesting that systematic hypometria of large saccades is a consequence of saccade programming (Vitu et al., 2017). Second, the maximal target eccentricity we used was of 41°, which may have restricted the maximal saccade amplitude participants would have been able to make. Stahl (1999) showed that the average eye-only range when a target was presented at 50° was of about 35.9°, and in his paper of 2001, he confirmed these findings reporting an average amplitude of about 30.2° for the same target eccentricity. We are therefore confident that our technique did not significantly underestimate participants EOMR.

7. Conclusions

To summarize, across 3 experiments we have shown that covert, exogenous attention is impaired when targets are presented beyond the range of saccadic eye-movements but covert endogenous attention is preserved. These results are in accordance with previous studies with patients with defective oculomotor control and with neurotypical participants in an eyeabduction situation. We hypothesise that presenting a peripheral cue beyond the EOMR elicits different representations of the location of the stimulus in the visual and oculomotor system. These representations compete with one another, thus prolonging the time required to select the cued location and abolishing the processing advantage typically associated with valid peripheral cues. We conclude that only covert, exogenous attention is dependent on the activation of the oculomotor system, consistent with the weak, exogenous-only version of premotor theory proposed by Smith and Schenk (2012).

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REFERENCES

- Andersen, R. A. (1989). Visual and eye movement functions of the posterior parietal cortex. Annual Review of Neuroscience, 12, 377–403. https://doi.org/10.1146/annurev.ne.12.030189.002113.
- Awh, E., Armstrong, K. M., & Moore, T. (2006). Visual and oculomotor selection: Links, causes and implications for spatial attention. Trends in Cognitive Sciences, 10(3), 124–130. https://doi.org/10.1016/j.tics.2006.01.001.
- 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.
- Balslev, D., Newman, W., & Knox, P. C. (2012). Extraocular muscle afferent signals modulate visual attention eye proprioception and visual attention. *Investigative Ophthalmology & Visual Science*, 53(11), 7004–7009.
- Bao, Y., Lei, Q., Fang, Y., Tong, Y., Schill, K., Poppel, E., et al. (2013). Inhibition of return in the visual field the eccentricity effect is independent of cortical magnification. *Experimental Psychology*, 60(6), 425–431. https://doi.org/10.1027/1618-3169/ a000215.
- Bao, Y., & Pöppel, E. (2007). Two spatially separated attention systems in the visual field: Evidence from inhibition of return. *Cognitive Processing*, 8(1), 37–44. https://doi.org/10.1007/s10339-006-0151-x.
- Bao, Y., Wang, Z. Y., Liang, W., Wang, Y., Poppel, E., & Li, H. (2013). Inhibition of return at different eccentricities in the visual field share the same temporal window. *Neuroscience Letters*, 534, 7–11. https://doi.org/10.1016/j.neulet.2012.11.046.
- Beauchamp, M. S., Petit, L., Ellmore, T. M., Ingeholm, J., & Haxby, J. V. (2001). A parametric fMRI study of overt and covert shifts of visuospatial attention. *Neuroimage*, 14(2), 310–321.
- Becker, W., & Fuchs, A. F. (1969). Further properties of the human saccadic system: Eye movements and correction saccades with and without visual fixation points. Vision Research, 9(10), 1247–1258. https://doi.org/10.1016/0042-6989(69)90112-6.
- Belopolsky, A. V., & Theeuwes, J. (2009). No functional role of attention-based rehearsal in maintenance of spatial working memory representations. Acta Psychologica, 132(2), 124–135.
- Belopolsky, A. V., & Theeuwes, J. (2010). No capture outside the attentional window. Vision Research, 50(23), 2543–2550. https:// doi.org/10.1016/j.visres.2010.08.023.

- Belopolsky, A. V., & Theeuwes, J. (2012). Updating the premotor theory: The allocation of attention is not always accompanied by saccade preparation. Journal of Experimental Psychology Human Perception and Performance, 38(4), 902.
- Belopolsky, A. V., Zwaan, L., Theeuwes, J., & Kramer, A. F. (2007). The size of an attentional window modulates attentional capture by color singletons. Psychonomic Bulletin & Review, 14(5), 934–938.
- Bisley, J. W., & Goldberg, M. E. (2010). Attention, intention, and priority in the parietal lobe annual review of neuroscience, vol 33 (vol. 33, pp. 1-21). Palo alto: Annual reviews.
- Bisley, J. W., Mirpour, K., Arcizet, F., & Ong, W. S. (2011). The role of the lateral intraparietal area in orienting attention and its implications for visual search. *European Journal of Neuroscience*, 33(11), 1982–1990. https://doi.org/10.1111/j.1460-9568.2011.07700.x.
- Boon, P. J., Theeuwes, J., & Belopolsky, A. V. (2017). Eye abduction reduces but does not eliminate competition in the oculomotor system. *Journal of Vision*, 17(5). https://doi.org/10.1167/17.5.15, 15-15.
- Born, S., Mottet, I., & Kerzel, D. (2014). Presaccadic perceptual facilitation effects depend on saccade execution: Evidence from the stop-signal paradigm. *Journal of Vision*, 14(3), 7. https://doi.org/10.1167/14.3.7.
- Champely, S. (2012). Package 'PWR'. Vienna, Austria: R Foundation for Statistical Computing.
- Cohen, J. (1988). Statistical power analysis for the behavioral sciences (2nd ed.). Hillsdale, NJ: Lawrence Erlbaum.
- Collins, T., & Dore-Mazars, K. (2006). Eye movement signals influence perception: Evidence from the adaptation of reactive and volitional saccades. Vision Research, 46(21), 3659–3673. https://doi.org/10.1016/j.visres.2006.04.004.
- 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.
- Graighero, 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 CB*, 14(4), 331–333. https://doi.org/10.1016/j.cub.2004.01.054.
- de Haan, B., Morgan, P. S., & Rorden, C. (2008). Covert orienting of attention and overt eye movements activate identical brain regions. Brain Research, 1204, 102–111. https://doi.org/10.1016/ j.brainres.2008.01.105.
- 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.
- 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., Wolf, W., & Hauske, G. (1986). Adaptive gain control of saccadic eye movements. Human Neurobiology, 5(4), 245–253.
- Dunne, S., Ellison, A., & Smith, D. T. (2015). Rewards modulate saccade latency but not exogenous spatial attention. Frontiers in Psychology, 6, 1080. https://doi.org/10.3389/ fpsyg.2015.01080.
- Frost, D., & Pöppel, E. (1976). Different programming modes of human saccadic eye movements as a function of stimulus eccentricity: Indications of a functional subdivision of the visual field. Biological Cybernetics, 23(1), 39–48. https://doi.org/ 10.1007/BF00344150.
- Gabay, S., Henik, A., & Gradstein, L. (2010). Ocular motor ability and covert attention in patients with Duane retraction syndrome. *Neuropsychologia*, 48(10), 3102–3109. https://doi.org/ 10.1016/j.neuropsychologia.2010.06.022.

- 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.
- Guitton, D., & Volle, M. (1987). Gaze control in humans: Eye-head coordination during orienting movements to targets within and beyond the oculomotor range. *Journal of Neurophysiology*, 58(3), 427–459.
- Henson, D. B. (1978). Corrective saccades: Effects of altering visual feedback. Vision Research, 18(1), 63–67. https://doi.org/10.1016/ 0042-6989(78)90078-0.
- Hoffman, J. E., & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Perception & Psychophysics*, 57(6), 787–795.
- Hunt, A. R., & Kingstone, A. (2003). Covert and overt voluntary attention: Linked or independent? *Cognitive Brain Research*, 18(1), 102–105.
- Hüttermann, S., Bock, O., & Memmert, D. (2012). The breadth of attention in old age. Ageing Research, 3(1), 10.
- Ignashchenkova, A., Dicke, P. W., Haarmeier, T., & Thier, P. (2004). Neuron-specific contribution of the superior colliculus to overt and covert shifts of attention. Nature Neuroscience, 7(1), 56–64.
- 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. https://doi.org/10.1093/cercor/bhn001.
- 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., Blohm, G., Pisella, L., & Munoz, D. P. (2015). Saccade execution suppresses discrimination at distractor locations rather than enhancing the saccade goal location. *The European Journal of Neuroscience*, 41(12), 1624–1634. https://doi.org/ 10.1111/ejn.12923.
- Klein, R. M. (1980a). Does oculomotor readiness mediate cognitive control of visual attention? In R. S. Nickerson (Ed.), Attention and performance VIII (p. 17). Hillsdale, NJ: Erlbaum.
- Klein, R. M. (1980b). 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., & Pontefract, A. (1994a). Does oculomotor readiness mediate cognitive control of visual-attention – revisited Attention and performance Xv (Vol. 15, pp. 333–350). Cambridge: M I T PRESS.
- Klein, R. M., & Pontefract, A. (1994b). Does oculomotor readiness mediate cognitive control of visual attention? Revisited! Attention and performance XV: Conscious and nonconscious information processing (p. 333).
- Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming of saccades. Vision Research, 35(13), 1897–1916.
- Lawrence, Michael A. (2011). ez: Easy Analysis and Visualization of Factorial Experiments. Computer software manual](R package version 3.0–0).
- Lupiáñez, J., Milliken, B., Solano, C., Weaver, B., & Tipper, S. P. (2001). On the strategic modulation of the time course of facilitation and inhibition of return. The Quarterly Journal of Experimental Psychology Section A, 54(3), 753–773.
- MacLean, M. H., & Giesbrecht, B. (2015). Neural evidence reveals the rapid effects of reward history on selective attention. Brain Research, 1606, 86–94.
- MacLean, G. H., Klein, R. M., & Hilchey, M. D. (2015). Does oculomotor readiness mediate exogenous capture of visual attention? Journal of Experimental Psychology Human Perception and Performance, 41(5), 1260–1270.
- Michalczyk, Ł., Paszulewicz, J., Bielas, J., & Wolski, P. (2018). Is saccade preparation required for inhibition of return (IOR)?

Neuroscience Letters, 665, 13-17. https://doi.org/10.1016/j. neulet.2017.11.035.

- 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 Sciences, 98(3), 1273–1276.
- Morgan, E. J., Ball, K., & Smith, D. T. (2014). The role of the oculomotor system in covert social attention. Attention Perception & Psychophysics, 76(5), 1265–1270.
- 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.
- Müri, 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., & Pierrot-Deseilligny, 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.
- Niederhauser, S., & Mojon, D. S. (2002). Normal isopter position in the peripheral visual field in goldmann kinetic perimetry. *Ophthalmologica*, 216(6), 406–408, 67554.
- 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. https://doi.org/ 10.1006/nimg.2000.0539.
- Odoj, B., & Balslev, D. (2016). Role of oculoproprioception in coding the locus of attention. Journal of Cognitive Neuroscience, 28(3), 517–528.
- Paap, K. R., & Ebenholtz, S. M. (1976). Perceptual consequences of potentiation in the extraocular muscles: An alternative explanation for adaptation to wedge prisms. Journal of Experimental Psychology Human Perception and Performance, 2(4), 457.
- Perry, R. J., & Zeki, S. (2000). The neurology of saccades and covert shifts in spatial attention: An event-related fMRI study. Brain, 123(Pt 11), 2273–2288.
- Pierce, J. W. (2009). Generating stimuli for neuroscience using PsychoPy. Frontiers in Neuroinformatics, 2(10). https://doi.org/ 10.3389/neuro.11.010.2008.
- Posner, M. I. (1980). Orienting of attention. Quarterly Journal of Experimental Psychology, 32(FEB), 3–25.
- Posner, M. I., & Cohen, Y. (1980). Attention and the control of movements. *Tutorials in Motor Behavior*, 243–258.
- Rafal, R. D., Henik, A., & Smith, J. (1991). Extrageniculate contributions to reflex visual orienting in normal humans: A temporal Hemifield advantage. *Journal of Cognitive Neuroscience*, 3(4), 322–328. https://doi.org/10.1162/ jocn.1991.3.4.322.
- 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(Pt 2), 267–280.
- Rizzolatti, G., Riggio, L., Dascola, I., & Umilta, 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 Attention and performance Xv (Vol. 15, pp. 231–265).
- Robinson, D. A. (1973). Models of the saccadic eye movement control system. Kybernetik, 14(2), 71–83. https://doi.org/ 10.1007/BF00288906.
- Rovamo, J., & Virsu, V. (1979). An estimation and application of the human cortical magnification factor. *Experimental Brain Research*, 37(3), 495–510.
- Sato, T. R., & Schall, J. D. (2003). Effects of stimulus-response compatibility on neural selection in frontal eye field. *Neuron*, 38(4), 637–648.

- 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(2–3), 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. Attention and Performance XIX Common Mechanisms in Perception and Action, 19, 609–627.
- Sheliga, B. M., Riggio, L., & Rizzolatti, G. (1994). Orienting of attention and eye-movements. *Experimental Brain Research*, 98(3), 507–522.
- Shepherd, M., Findlay, J. M., & Hockey, R. J. (1986). The relationship between eye-movements and spatial attention. *The Quarterly Journal of Experimental Psychology Section A*, 38(3), 475–491.
- Smith, D. T., Ball, K., & Ellison, A. (2014). Covert visual search within and beyond the effective oculomotor range. Vision Research, 95, 11–17. https://doi.org/10.1016/ j.visres.2013.12.003.
- Smith, D. T., Ball, K., Ellison, A., & Schenk, T. (2010). Deficits of reflexive attention induced by abduction of the eye. *Neuropsychologia*, 48(5), 1269–1276. https://doi.org/10.1016/ j.neuropsychologia.2009.12.028.
- Smith, D. T., & Casteau, S. (2018). The effect of offset cues on saccade programming and covert attention. Quarterly Journal of Experimental Psychology. https://doi.org/10.1177/ 1747021818759468.
- 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. (2009a). An intact eyemovement system is not required to generate Inhibition of Return. Journal of Neuropsychology, 3(2), 5.
- Smith, D. T., Jackson, S. R., & Rorden, C. (2009b). 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 CB, 14(9), 792–795. https://doi.org/ 10.1016/j.cub.2004.04.035.
- Smith, D. T., & Schenk, T. (2012). The Premotor theory of attention: Time to move on? *Neuropsychologia*, 50(6), 1104–1114.
- Smith, D. T., Schenk, T., & Rorden, C. (2012). Saccade preparation is required for exogenous attention but not endogenous attention or IOR. Journal of Experimental Psychology Human Perception and Performance, 38(6), 1438–1447. https://doi.org/ 10.1037/a0027794.
- Stahl, J. S. (1999). Amplitude of human head movements associated with horizontal saccades. Experimental Brain Research, 126(1), 41–54. https://doi.org/10.1007/ s002210050715.
- Steele, J. C., Richardson, J. C., & Olszewski, J. (1964). Progressive supranuclear palsy. A heterogeneous degeneration involving the brain stem, basal ganglia and cerebellum with vertical gaze and pseudobulbar palsy, nuchal dystonia and dementia. *Archives of Neurology*, 10, 333–359.
- Taylor, P. C. J., Nobre, A. C., & Rushworth, M. F. S. (2007). FEF TMS affects visual cortical activity. *Cerebral Cortex*, 17(2), 391–399.
- 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), 114–118.
- 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.

- Van der Stigchel, S., & Theeuwes, J. (2005). The influence of attending to multiple locations on eye movements. Vision Research, 45(15), 1921–1927. https://doi.org/10.1016/j.visres.2005.02.002.
- Vitu, F., Casteau, S., Adeli, H., Zelinsky, G. J., & Castet, E. (2017). The magnification factor accounts for the greater hypometria

and imprecision of larger saccades: Evidence from a parametric human-behavioral study. *Journal of Vision*, 17(4). https://doi.org/10.1167/17.4.2, 2-2.

Wickham, H. (2009). ggplot2: Elegant graphics for data analysis. New York: Springer-Verlag.