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Covert visual search within and beyond the effective oculomotor range

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Abstract

Covert spatial attention is tightly coupled to the eye-movement system, but the precise nature of this coupling remains contentious. Recent research has argued that covert attention and overt eye-movements may share a common biological limit, such that covert exogenous orienting of attention is limited to stimuli that fall within the range of possible eye movements (the effective oculomotor range: EOMR). However, this conclusion is based on a single experimental paradigm: The Posner cueing task. Here, we examine the extent to which covert spatial attention is limited to the EOMR in visual search. Exogenous attention was assessed using a feature search task and endogenous attention assessed using a conjunction search task. The tasks were performed monocularly with the dominant eye in the frontal position or abducted by 40 degrees. In the abducted position stimuli in the temporal hemispace could be seen, but could not become the goal of a saccadic eye-movement (i.e. they were beyond the EOMR). In contrast, stimuli in the nasal hemifield remained within the EOMR. We observed a significant effect of eye-abduction on feature search, such that search was slower when targets appeared beyond the EOMR. In contrast, eye-abduction had no effect on search times during conjunction search. Set size did not interact with target location or eye-position. It is concluded that optimal covert orienting of exogenous attention in visual search is restricted to locations within the effective oculomotor range.

Keywords:

attention; exogenous; eye movement; endogenous; oculomotor; covert visual search

1. Introduction

There is considerable evidence for a tight coupling between covert attention and overt eye-movements (Awh, Armstrong, & Moore, 2006; Smith & Schenk, 2012). Behaviourally, saccadic eye-movements are preceded by a mandatory shift of attention to the saccade goal (Deubel, 2008; Dore-Mazars, Pouget, & Beauvillain, 2004; Hoffman & Subramaniam, 1995; Shepherd, Findlay, & Hockey, 1986), and attention and eye-movements activate overlapping brain areas including the Frontal Eye Fields (FEF) and Intraparietal Sulcus (IPS) (Corbetta et al., 1998; de Haan, Moryan, & Rorden, 2008; Fairhall, Indovina, Driver, & Macaluso, 2009; Gitelman, Parrish, Friston, & Mesulam, 2002; Nobre, Gitelman, Dias, & Mesulam, 2000; Perry & Zeki, 2000). Furthermore, TMS over these regions interferes with eye-movements (e.g. Zangemeister, Canavan, & Hoemberg, 1995) and covert spatial attention (Ellison, Schindler, Pattison, & Milner, 2004; Grosbras & Paus, 2002; Muggleton, Juan, Cowey, & Walsh, 2003; O'Shea, Muggleton, Cowey, & Walsh, 2004; Smith, Jackson, & Rorden, 2005). In addition electrophysiological stimulation of FEF elicits both eye-movements and shifts of attention (Armstrong, Fitzgerald, & Moore, 2006; Armstrong & Moore, 2007; Moore & Armstrong, 2003; Moore & Fallah, 2001; Silvanto, Lavie, & Walsh, 2006). However, the exact nature of the link between overt and covert attention remains contentious, and several papers have reported dissociations between activation of the eye-movement system and attentional orienting (Belopolsky & Theeuwes, 2009, 2012; Hunt & Kingstone, 2003; Klein, 1980; Klein & Pontefract, 1994; Smith, Rorden, & Schenk, 2012).

One proposal made by Craighero, et al., (2004) is that attention and eye-movements share a common stop-limit, such that covert attention cannot be oriented beyond the effective oculomotor range (EOMR). The EOMR refers to the range of locations that a participant can fixate by making a saccadic eye-movement without also needing to make a head movement and is neutrally limited to $\sim 45^\circ$ (Guitton & Volle, 1987). This proposal was based on the eye abduction paradigm, in which the execution of eye-movements was prevented by presenting stimuli beyond the EMOR. Specifically, participants were asked to abduct the eye by 40 degrees into the temporal hemispace, such that

they fixated a point near the limit of their oculomotor range (see Figure 1a). A central, predictive cue indicated a location in either the nasal hemispace (which was within the EOMR) or temporal hemispace (beyond the EOMR) in which the probe would appear. Craighero et al., observed weaker cueing effects in the temporal hemifield than the nasal hemifield and concluded that endogenous attention was tightly linked to the ability to execute eye-movements. These data were consistent with their previous study of patients with VIth nerve palsy, who had a deficit of attention when viewing stimuli with the palsied eye but not with the healthy eye (Craighero, Carta, & Fadiga, 2001).

However, studies of other patients with defective eye-movements have produced a different pattern of results. Specifically, Smith et al., (2004) reported a single case with congenital ophthalmoplegia (i.e. the inability to make any eye-movements). This patient had impaired exogenous attention, but contrary to Craighero (2001), intact endogenous attention. A subsequent study by Gabay, Henik & Gradstein (2010) examined exogenous and endogenous attention in patients with Duane's Retraction Syndrome (a developmental disorder which limits the ability to make abductive eye-movements). Consistent with the findings of Smith et al., (2004), these patients exhibited a deficit of exogenous attention but intact endogenous attention. Furthermore, we recently used the eye-abduction paradigm to compare the effect of placing stimuli beyond the EOMR paradigm on exogenous and endogenous attention using a variant of the Posner cueing task (Smith et al., 2012). As with the patient studies, our participants showed a deficit of exogenous attention when a peripheral luminance change which appeared beyond the EOMR was used as the attentional cue. However, when attention was cued with a centrally presented, symbolic cue (in this case a number) endogenous attention was unaffected. It was concluded that the ability to execute eye-movements is necessary for exogenous attention, but not endogenous attention. It is not clear why we and others have been unable to replicate the Craighero et al. finding of impaired endogenous attention for locations beyond the EOMR. However, the fact that they found such a result suggests that further studies investigating the impact of placing stimuli beyond the EOMR on covert attention are

required in order to draw secure conclusions about the relationship between the EOMR and the different modes of spatial attention.

One way to address this issue is to investigate the extent to which the dissociation between exogenous and endogenous attention observed in cueing tasks generalises to other attention paradigms, such as visual search. The difficulty of a search task depends on the degree of similarity between target and distracters. Targets defined by a single feature (e.g. an oblique line among vertical lines) are typically easy to detect, and detection times are unaffected by the number of competing items. This type of easy, feature search is mediated by fast, reflexive mechanisms akin to those that mediate exogenous attention. In contrast, targets defined by a unique conjunction of features placed among distracters which share only one feature of the unique conjunction (e.g. a red oblique line among red vertical lines and green oblique lines) are much harder to detect, resulting in search times that increase with the number of distracters. This conjunction search requires the deployment of voluntary, effortful processes akin to endogenous attention (Treisman & Gelade, 1980; Wolfe, 1994).

If the dissociation between exogenous and endogenous attention with respect to their coupling with the EOMR generalises beyond cueing tasks, limiting the ability to execute eye-movements should have a much greater impact on feature search (which engages exogenous attention) than it does on conjunction search (which relies on endogenous attention). In a recent study we attempted to address this issue by examining the effect of eye-abduction on covert visual search for feature targets (Smith, Ball, Ellison, & Schenk, 2010). In one experiment participants knew the identity of the target and in another the identity was not known. In both tasks it took longer to detect targets when they lay beyond the range of eye-movements, which we argued was evidence of a deficit of exogenous attention. In a 3rd experiment we changed the distractor stimuli, such that they were more heterogeneous and more similar to the target. In this task, while there was no slowing of reaction time, there was a reduction in accuracy. We interpreted these findings as evidence that exogenous attention is limited to the EOMR.

However, it is necessary to be cautious in interpreting these data too strongly for two reasons. Firstly, we only utilised one set-size, and it is therefore unclear whether disrupting eye-movements imposed a stable cost on search (i.e. search is slowed but still parallel), or whether this cost would vary with the number of distractors (i.e. search must engage voluntary attention to compensate for the impairment to reflexive search). Secondly, our 3rd experiment did not elicit an RT cost but did elicit a deficit in response accuracy. Pilot testing suggested that this search task actually produced a shallow search slope (13ms/item) and it might be argued that this task engaged some voluntary attentional mechanisms. However, without multiple set-sizes and a clearly serial search, it is not possible to determine which attentional systems were disrupted in this task.

To summarize, the finding that covert exogenous attention is tightly coupled to the ability to execute eye-movements has been replicated by several groups using several different experimental paradigms. However, the extent to which covert endogenous attention is similarly restricted to the EOMR is more controversial. Here, we use the eye-abduction technique to examine whether the independence between eye-movements and covert, endogenous attention observed by Smith et al., (2012), Gabay et al., (2010), Klein et al., (1980), Hunt & Kingstone (2003) and Rafal et al., (1988) in cueing tasks generalises to other paradigms that measure exogenous and endogenous attention, specifically feature and conjunction search.. If the eye-movement system is required for feature but not conjunction search, search for targets appearing in the temporal hemispace (i.e. beyond the range of eye-movements) in the eye-abducted condition should be disrupted during feature search whereas conjunction search should be unaffected.

2. Methods

2.1. Participants

There were 19 participants (10 female, 5 left handed, 3 left eyed). Ages ranged from 19 to 44 (median 26). All participants had normal vision (assessed by self-report) or wore contact lenses. Nine participants completed the feature search task and ten completed the conjunction search task.

2.2. Apparatus

Stimuli were generated using a Cambridge Research Systems ViSaGe graphics card and displayed on a 17-inch Sony Trinitron CRT monitor with a refresh rate of 100Hz. Responses were collected using a two-button button-box. Fixation was monitored using a BioPac 150 recording EOG at 250 Hz. A laser pointer was attached to the centre of the forehead of the participant to allow the experimenter to monitor head position. If participants moved their head to reduce the angle of abduction of the eye the experimenter would tell them to return to the correct position and record the number of the trial. The head was supported by a chinrest.

2.3.1. Stimuli: Feature Search

The search array consisted of white rectangles (10 x 40 pixels) and a white fixation point (5x5 pixels) on a grey (23cdm²) background. The positions of the rectangles were randomized with the constraints that least 3 bars always appeared on each side of the display and bars could not appear within 3.5° of the vertical or horizontal midlines, beyond 11° of the vertical midline or beyond 7.5° of the horizontal midline. The orientation of the rectangles was randomized across trials. On half the trials the bars were oriented at an angle of 45° and on the other half they were oriented at an angle of 335°. The target was a white rectangle (10 x 40 pixels) which was oriented orthogonally to the other stimuli in the display. Search arrays contained 6, 12 or 18 items. On target-present trials the target was presented instead of one of the distractor items. Targets appeared with equal frequency on the left and right sides of the display.

2.3.2. Stimuli: Conjunction Search

The search array consisted of blue bars oriented at an angle of 45° ($1^\circ \times 1.5^\circ$, 32cdm^2), yellow bars oriented at 335° ($1^\circ \times 1.5^\circ$, 36cdm^2) and a white fixation point (5x5 pixels) on a grey (23cdm^2) background. The probe was a yellow bar oriented at 45° ($1^\circ \times 1.5^\circ$, 36cdm^2). The positions of the rectangles were randomized, with the constraints in their location the same as in the feature search. Arrays comprised 6, 12 or 18 items. On target-present trials the target was presented instead of one of the distractor items. Targets appeared with equal frequency on the left and right sides of the display.

2.4. Procedure

Eye dominance was assessed for each participant by having them sit ~2 meters away from the experimenter and fixate on the nose of the experimenter. Participants were then told to extend their arms and bring their hands together in front of the eyes leaving only a small gap through which the experimenter could see one of the participants' eyes. The visible eye was recorded as dominant. The eye tracker was calibrated at the start of the experimental trials.

Participants performed the task monocularly with the dominant eye. The nondominant eye was patched. Participants were positioned 57cm away from the display with their head resting in a chinrest. They were instructed to fixate the central fixation point and not to move their eyes during a trial. On each trial the fixation point appeared for 1000ms, followed by the search array. Participants were required to press one of two buttons to indicate whether the target was present or absent. The search array was present until the participant made a response. Targets appeared on 75% of trials and with equal frequency in the nasal hemifield (Nasal condition) and temporal hemifield (Temporal condition).

Participants performed either the feature search task or the conjunction search task. Each participant completed 1 block of 48 practice trials and 6 blocks of 48 experimental trials. Participants completed 3 blocks of trials in the Eye-Frontal condition, where the eye was in the centre of the orbit, and 3 blocks of trials in the Eye-Abducted condition. Eye frontal and Eye abducted blocks were

interleaved. In the Abducted condition the participant fixated the centre of the display and the head and body were rotated to the right when the left eye was in use and to the left when the right eye was in use. This manipulation produced an abduction of the eye of 40° away from the trunk and head midline. The response box was placed along the horizontal midline of the body and oriented vertically such that the target-present button was above the target absent button. Participants responded with the preferred hand. Participants were instructed to respond as quickly as possible.

Figure 1 illustrates the experimental setup.

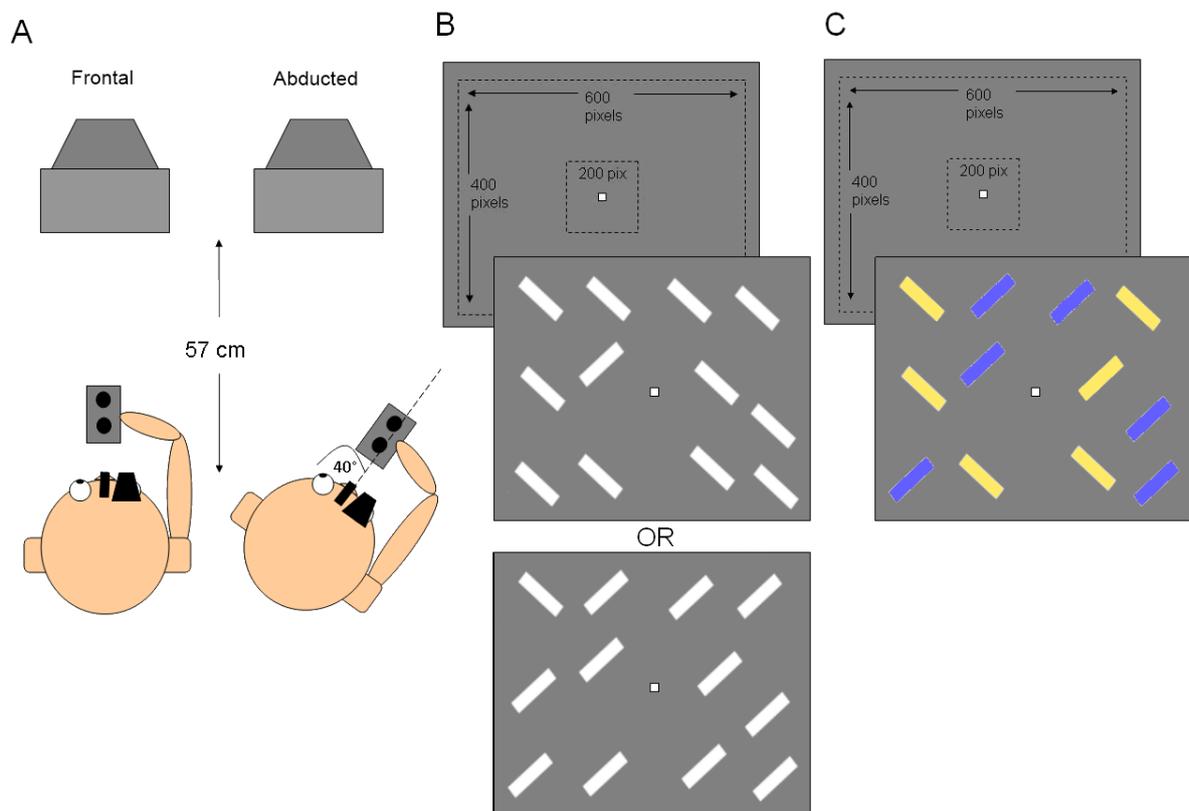


Figure 1: Experimental setup and procedure. Panel A shows the setup of the apparatus in the Eye-Frontal and Eye-Abducted conditions. In this example the right eye is occluded by an eye-patch and the right hand is used for responses. Fixation was controlled using EOG. The dotted line shows the direction of the laser pointer attached to the forehead. Panel B shows the sequence of events during the feature search. Panel C shows the sequence of events of the conjunction search. The dotted lines were not visible during the experiment.

3. Results

One participant in the conjunction search group had reaction times that were > 3SD longer than the group mean. This participant was excluded from the analysis. The remaining data, nine participants in each group, were filtered to remove trials in which participants had broken fixation (2.1%) or had moved their head (0.3%). Anticipations (responses faster than 100ms) and outliers that were more than 2.5 standard deviations greater than an individual's mean reaction time were also excluded (3.4%).

3.1. Data Analysis: Reaction Time

Correct responses to target present trials were analysed. Mean reaction times were subjected to a 2x3x2x2 mixed model ANOVA with within-subjects factors of Eye Position (Frontal vs Abducted), Set Size (6, 12, 18) and Hemifield of Probe (Nasal vs Temporal Hemifield) and a between-subjects factor of Search Type (Feature vs Conjunction). The ANOVA revealed a main effect of Set Size ($F_{(2,16)} = 13.4$, $P < 0.05$), a significant 2-way interaction between Set Size and Search Type ($F_{(2,34)} = 21.16$, $P < 0.05$) and a significant 3-way interaction between Eye Position, Hemifield of Probe and Search Type ($F_{(2,16)} = 9.95$, $P < 0.05$). Further analysis of the Set Size x Search Type interaction (2 way ANOVA with a factor of Set Size at each level of Search Task) revealed a main effect of Set Size for the Conjunction search task, such that RT increased with set size ($F_{(1,8)} = 24.17$, $P < 0.05$) but no effect of Set Size on the Feature search task ($F_{(1,8)} = 0.76$, $P = 0.48$).

The significant 3-way interaction between Eye Position, Hemifield of Probe and Search Type was broken down into a 2 (Eye-Position) x 2 (Hemifield of probe) repeated measures ANOVA at each level of Search Type. For Conjunction search the ANOVA revealed no significant main effects or interactions. In contrast, for Feature search the ANOVA revealed a main effect of Hemifield ($F_{(1,8)} = 20.37$, $P < 0.05$) and, critically, a significant Hemifield x Eye Position interaction ($F_{(1,8)} = 7$, $P < 0.05$). Inspection of Figure 2 suggests this interaction was driven by slower search times when the eye was abducted, but only for probes in the temporal hemispace. Planned comparisons (t-tests with a

bonferroni correction) confirm this impression: feature search was significantly slower in the temporal hemispace in the eye-abducted condition (Nasal = 662ms, Temporal = 730ms; $t_{(8)} = 4.09$, $p < 0.012$), but not in the frontal condition (Nasal = 650ms, Temporal = 663ms; $t_{(8)} = 1.30$, $p = 0.229$).

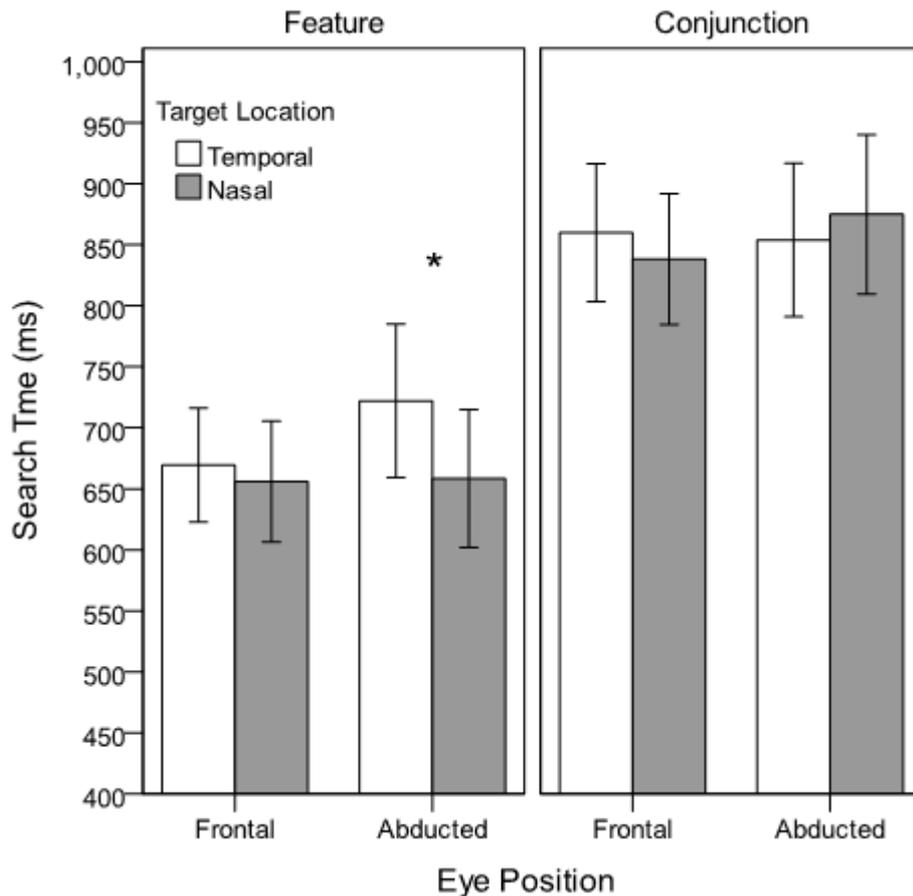


Figure 2: Mean correct reaction times on target-present trials. Eye-abduction led to a systematic slowing of feature search when probes appeared in the temporal hemispace. The same manipulation had no effect on conjunction search. The asterisk indicates a significant difference $p < 0.05$. Error bars show ± 1 SEM.

3.2. Data Analysis: Accuracy

Mean hit rates were subjected to a $2 \times 3 \times 2 \times 2$ mixed model ANOVA with within-subjects factors of Eye Position (Frontal vs Abducted), Set Size (6, 12, 18) and Hemifield of Probe (Nasal vs Temporal Hemifield) and a between-subjects factor of Search Type (Feature vs Conjunction). The ANOVA revealed a main effect of Set Size ($F_{(2,16)} = 9.01$, $P < 0.05$), such that accuracy declined with increasing set-size, a main effect of Hemifield of Probe ($F_{(2,16)} = 5.41$, $P < 0.05$), such that accuracy was

worse in the Temporal hemifield than the Nasal hemifield (89% vs 92%) and a significant 2-way interaction between Set Size and Search Type ($F_{(2,34)}=5.57, P<0.05$). Further analysis of the Set Size x Search Type interaction (ANOVA with a factor of Set Size at each level of Search Task) revealed a main effect of Set Size for the Conjunction search task, such that accuracy decreased with set size ($F_{(1,8)}=8.61, P<0.05$) but no effect of Set Size on the Feature search task ($F_{(1,8)}=0.65, P=0.53$). These effects are illustrated in Figure 3.

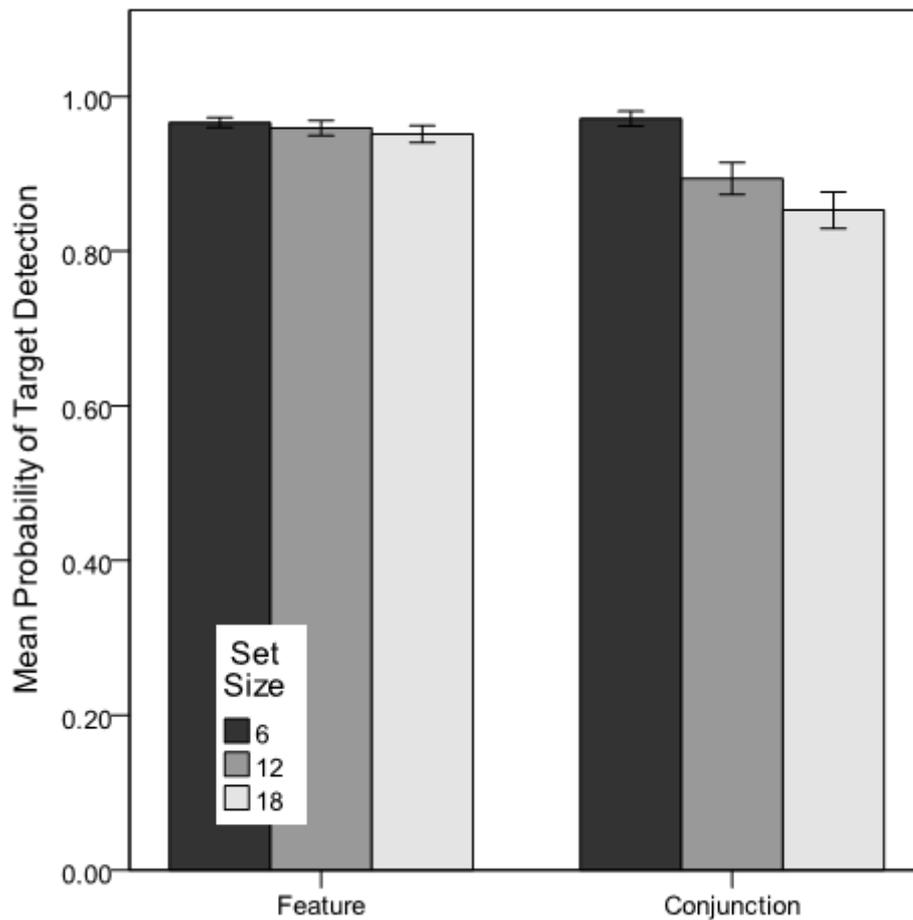


Figure 3: Probability of detecting a target. Accuracy during feature search was close to ceiling and did not vary with set size. In contrast, accuracy during conjunction search significantly declined with increasing set size. Error bars show +/-1 SEM.

3.4. Data Analysis: Target Absent Trials

Data were collapsed across hemifield for this analysis because correct responses to target-absent trials cannot sensibly be assigned to a hemifield, and for false alarm trials it is not possible to

know where participants perceived the target to have appeared. Table 1 shows False Alarm rates for each set size at each level of eye-position for the two search tasks. Only target absent trials were included in the analysis. Analysis of False Alarms showed no significant main effects but there was a Task x Set Size interaction ($F_{(2,32)} = 4.5, p < 0.05$), such that FA rate increased with set size during conjunction search, whereas it decreased with set size during feature search. Note that FA rate was not affected by the eye position manipulation.

Table 1: Mean probability of a false alarm for each set size in the different search tasks at each level of eye-position, collapsed across hemifields.

	Set Size	Eye Frontal			Eye Abducted		
		6	12	18	6	12	18
Feature		0.10	0.08	0.06	0.14	0.07	0.06
Conjunction		0.08	0.13	0.18	0.10	0.16	0.20

4. Discussion

The goal of this study was to investigate the extent to which covert visual search was restricted to the effective oculomotor range. The results show a clear effect of eye-abduction on feature search, such that reaction times were slower when targets lay beyond the range of saccadic eye movements. The magnitude of this slowing was not systematically affected by set size. In contrast, while conjunction search was affected by set-size, such that search was slower with increasing number of distractors, search times were unaffected when targets lay beyond the range of eye-movements.

These data are broadly consistent with our previous studies (Smith, Ball, Ellison, & Schenk, 2010; Smith, Rorden, & Jackson, 2004; Smith et al., 2012), and extends them in two important ways. Firstly, these results show that the dissociation between exogenous and endogenous attention with respect to the role of the oculomotor system previously observed in cueing tasks generalises to visual search tasks in which there is no predictive symbolic cue. Given that there is some

inconsistency between the previous studies of Craighero and colleagues (Craighero et al., 2001; Craighero et al., 2004), and other groups (Gabay et al., 2010; Hunt & Kingstone, 2003; Klein, 1980; Klein & Pontefract, 1994; Smith & Schenk, 2012) with respect to the role of the oculomotor system in endogenous attention, our result offers important, convergent evidence that exogenous attention is dependent on the oculomotor system whereas endogenous attention is largely independent of oculomotor control (see also (Belopolsky & Theeuwes, 2009, 2012). These data are also convergent with our recent findings from visuospatial working memory, which demonstrate that optimal memory for sequences of salient locations is dependent on the oculomotor system, whereas memory for locations indicated by a symbolic cue is independent of the eye-movement system (Ball, Pearson, & Smith, 2013). Secondly, by using multiple set sizes we established that the inability to move the eyes resulted in a fixed cost on feature search of ~60-70ms. This contrasts with our previous suggestion that the cost of eye-abduction would increase with set size increase as participants became more dependent on endogenous attentional mechanisms (Smith et al., 2010). One speculative interpretation of this finding is that placing salient objects beyond the EOMR interfered with the generation of a priority map (Fecteau & Munoz, 2006) by preventing the oculomotor system contributing to the process of biased competition (e.g. Bisley, Mirpour, Arcizet, & Ong, 2011; Duncan, 2006).

It remains unclear why it has been impossible to replicate the association between endogenous attention and EOMR reported by Craighero et al., (2004). One possibility is that the cue stimulus used by Craighero (a pointer lateralised to the left or right of fixation) acted like an arrow cue. Recent studies have shown that arrow cues engage both exogenous and endogenous attentional mechanisms (Ristic & Kingstone, 2006; Tipples, 2002). It may be that in Craighero et al., (2004) eye-abduction disrupted the exogenous component of the cue, thus reducing the overall cueing effect to a level below what was detectable by their protocol. In this context it is worth noting that in Craighero et al., (2004) neither the main effect of Cue Validity or the Hemifield x Validity interaction were statistically significant in the eye-abducted condition; $p > 0.05$ [the actual value is

not reported] and $p=0.18$, respectively), suggesting that their cueing effects were rather weak. Consistent with the idea that disruption to the oculomotor system impairs the reflexive component of arrow cueing, Rafal et al., (1988) observed that arrow cueing effects in PSP patients with vertical gaze paralysis were smaller in the vertical dimension than horizontal dimension. Examining the effect of eye-abduction on non-predictive arrow cues would provide a direct test of the link between the oculomotor system and the reflexive component of arrow cueing.

From a theoretical perspective, we have argued that eye-abduction disrupts both planning and execution of saccadic eye-movements, and so offers a test of the Premotor theory of attention (Rizzolatti, Riggio, Dascola, & Umiltà, 1987; Rizzolatti, Riggio, & Sheliga, 1994) which argues that the planning of saccadic eye-movements is necessary and sufficient for covert endogenous attention. Our finding that endogenous attention can be freely oriented to locations that cannot become the goal of a saccade suggests that the strong version of the premotor theory cannot be true. However, a weaker version of the theory, that activation of the oculomotor system is required for exogenous attention but not necessary to generate endogenous shifts of attention is consistent with our results (Klein, 1980; Rafal, Posner, Friedman, Inhoff, & Bernstein, 1988; Smith & Schenk, 2012). This interpretation is based on the assumption that eye abduction prevents both planning and execution of all eye-movements. Proponents of the premotor theory might argue that participants were still able to plan combined eye-head movements to the targets beyond the range of eye-movements, and it was the preparation for a combined eye-head movement that mediated the endogenous attention shifts (e.g. Cicchini, Valsecchi, & de'Sperati, 2008). While this account is theoretically plausible, there is currently no evidence that preparing, but not executing, a head movement is sufficient to produce a shift of attention. Indeed, evidence from studies of eye-movements indicates that preparing but not executing a saccade is not sufficient to elicit a covert shift of attention (Hunt & Kingstone, 2003; Klein, 1980; Klein & Pontefract, 1994; Mottet, Kerzel, & Born, 2013). Furthermore, given the evidence that exogenous attention is associated with activation of the head-movement system (Corneil, Munoz, Chapman, Admans, & Cushing, 2008), it is not clear why the

preparation of head movements should support endogenous orienting but not exogenous orienting. We therefore suggest that although the capacity for covert preparation of head-movements to elicit shifts of attention remains an empirical question, planned combined eye-head movements are unlikely to be mediating endogenous attention in our experiment.

A second alternative possibility is that turning the trunk and head away from the vertical midline created a spatial bias in the direction of abduction- i.e. away from the temporal hemispace. For example Karnath and colleagues (Karnath, 1994; Karnath, Schenkel, & Fischer, 1991) have argued that spatial attention is anchored to the body midline, such that rotating the trunk towards the left attenuates spatial neglect. Subsequently, Grubb & Reed (2002) argued that trunk rotation affected attention in healthy participants, such that RTs were faster for stimuli that appear closer to the body midline relative to stimuli far from the midline, even when the stimuli are equidistant from fixation. A very similar finding was recently reported by Durand Camors, Trotter & Celebrini (2012), who argued that a trunk-centred bias in visual perception was driven by enhanced neuronal sensitivity when gaze direction was congruent with head and trunk orientation. In related work, Balslev, Gowen and Miall (2011) found that passive abduction of one eye shifted of the perceived midline in the direction of abduction and that reaction times to stimuli near the perceived midline were facilitated relative to RTs to stimuli further from the perceived midline.

While a spatial bias toward the trunk midline could produce a pattern of data similar to that observed in the feature search task, i.e. slower covert visual search for objects that are far from the trunk midline, it is necessary to be cautious when considering this account as an explanation for our data for several reasons. Firstly, Grubb et al., characterised their effect as a disengagement deficit (see Posner et al., 1994), such that participants had problems disengaging from an invalidly cued target which appeared far from the midline (i.e. impaired volitional re-orienting of attention). In contrast the data from our visual search task suggests participants were slower to reflexively engage attention to a salient target and had no problems when the task required serial engagement and disengagement. Secondly, eye-abduction only disrupted exogenous attention during search for a

salient target. There seems to be no obvious theoretical reason why a trunk-centred spatial bias should affect exogenous shifts of attention in feature search but not endogenous attention shifts in conjunction search. Thirdly, an effect of trunk rotation on attention in healthy participants was not observed by Karnath et al., (1991), or in a subsequent attempt to replicate the work of Grubb & Reed (Westwood, Jones, Cowper-Smith, & Klein, 2013), suggesting that trunk centred biases in attention can only be elicited under very specific experimental conditions. In contrast, the disruptive effect of presenting probes beyond the EOMR on covert attention is robust across different experimenters and different paradigms.

Although the primary measure of performance was reaction time (participants were told to prioritize speed of response) we also analysed participants' accuracy. There was a small but significant effect of hemifield, such that search was less accurate in the temporal hemifield (hit rates: Nasal = 92%, Temporal 89%). This bias was present for both feature and conjunction search but was not modulated by eye abduction. It is not clear why visual search should be less accurate in the temporal hemispace. The majority of participants used the right eye which meant the nasal hemifields projected to the right cerebral hemisphere. Given the well-established right hemisphere advantage for spatial attention (e.g. Corbetta & Shulman, 2002; Hausmann, 2005; Jewell & McCourt, 2000), one speculative possibility is that the small advantage for targets in the nasal hemifield reflects a subtle attentional bias towards the left side of space. However, we note that previous studies of hemispheric asymmetries in visual search typically report a right hemisphere advantage for conjunction search but not feature search (Michael & Ojeda, 2005; Palmer & Tzeng, 1990; Poynter & Roberts, 2012), whereas we found a right hemisphere advantage for both tasks.

To summarize, it has been shown that covert, exogenous shifts of attention to salient targets are impaired when the target lies beyond the effective oculomotor range. In contrast, endogenous shifts of attention during conjunction search are unaffected if the target is beyond the range of saccadic eye-movements. The finding that attentional capture in pop-out search is differentially affected by disruption to the eye-movement system is consistent with the majority of previous

cueing studies, which find that exogenous attention is limited to the effective oculomotor range, whereas endogenous attention is not (Gabay et al., 2010; Rafal et al., 1988; Smith et al., 2004; Smith et al., 2012). Evidence for a similar dissociation in spatial working memory has also recently been reported (Ball et al., 2013). These results provide converging evidence for the proposal that exogenous attention is tightly coupled to the oculomotor system whereas endogenous attention can be dissociated from oculomotor control (Smith & Schenk, 2012).

5. References

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