

available at [www.sciencedirect.com](http://www.sciencedirect.com)[www.elsevier.com/locate/brainres](http://www.elsevier.com/locate/brainres)
**BRAIN  
RESEARCH**

## Research Report

# Modulation of saccadic intrusions by exogenous and endogenous attention

E. Gowen<sup>a,\*</sup>, R.V. Abadi<sup>a</sup>, E. Poliakoff<sup>a</sup>, P.C. Hansen<sup>b</sup>, R.C. Miall<sup>b</sup>

<sup>a</sup>Faculty of Life Sciences, Moffat Building, The University of Manchester, PO Box 88, Sackville Street, Manchester, M60 1QD, UK

<sup>b</sup>University of Birmingham, UK

### ARTICLE INFO

#### Article history:

Accepted 6 January 2007

Available online 23 January 2007

#### Keywords:

Saccadic intrusion (SI)

Microsaccades

Fixation

Attention orienting

Inhibition of return

Exogenous attention

Endogenous attention

### ABSTRACT

Primary gaze fixation in healthy individuals is frequently interrupted by microsaccades and saccadic intrusions (SI). The neural systems responsible for the control of attention and eye movements are believed to overlap and in line with this, the behaviour of microsaccades appears to be affected by exogenous and endogenous attention shifts. In the current work we wished to establish whether SI would also be influenced by attention in order to provide evidence that SI and microsaccades exhibit similar behaviour and further investigate the extent of overlap between attention and eye movement systems. Twelve participants performed a cue–target task where they were cued exogenously or endogenously and had to respond to the appearance of a peripheral target with either a button press or saccade. Our results replicate earlier microsaccade research, indicating that SI are also influenced by exogenous and endogenous attention. In all conditions, SI frequency initially decreased following the cue, then rose to a maximum before falling to below baseline levels. Following the exogenous cue, SI were more frequently directed away from the cue as predicted by inhibition of return. Additionally, SI direction following the endogenous cue was biased towards the cue for the saccadic response mode only, suggesting that the degree to which the eye movement and attention systems overlap depends on whether an eye movement is required. In summary, our findings indicate that SI characteristics are modulated by exogenous and endogenous attention and in a similar way to microsaccades, suggesting that SI and microsaccades may lie on a continuum of fixational instabilities. Furthermore, as with microsaccades, SI are likely to provide additional insights into the relationship between attention and the oculomotor systems.

© 2007 Elsevier B.V. All rights reserved.

## 1. Introduction

### 1.1. Primary gaze fixation characteristics

Primary gaze fixation is never perfectly stable but consists of small involuntary physiological eye movements (Ditchburn, 1973; Carpenter, 1988). These are comprised of disconjugate

slow drifts (1–3' arc), small conjugate microsaccades (5–10' arc, 1–2 per second) and disconjugate tremors (15" arc, 30–80 Hz) (Ratliff and Riggs, 1950; Ditchburn, 1973; Steinman et al., 1982; Kowler, 1991). A further class of involuntary eye movement has also been described; saccadic intrusions (SI). SI consist of conjugate, horizontal saccadic eye movements that take the form of an initial fast eye movement away from the desired

\* Corresponding author.

E-mail address: [emma.gowen@manchester.ac.uk](mailto:emma.gowen@manchester.ac.uk) (E. Gowen).

eye position, followed after a variable duration by a return saccade or drift (Abadi and Gowen, 2004). However, it may be more appropriate to take the null hypothesis that there is no difference between SI and microsaccades. Indeed, recent work indicates that microsaccades are affected by the attentional requirements of the task (Hafed and Clark, 2002; Engbert and Kliegl, 2003a; Rolfs et al., 2004; Laubrock et al., 2005) and that SI characteristics such as amplitude and frequency also exhibit attentional modulation (Gowen et al., 2005). If further behavioural similarities are revealed between microsaccades and SI, this would provide additional support that they represent the same phenomena.

### 1.2. Attention and eye movements

Attention orienting is often divided into two forms: exogenous orienting occurs when attention is automatically drawn to a stimulus in a reflexively initiated or bottom-up manner and endogenous orienting occurs when attention is guided in a voluntary manner, by cognitive top-down mechanisms (Posner, 1980; Klein and Shore, 2000). Exogenous orienting develops within the first 100 ms after stimulus presentation, whereas the effects of endogenous attention are observed after 200–300 ms (Muller and Rabbitt, 1989). Findings from behavioural, lesion and imaging studies indicate that these forms of attention are mediated by separate neural substrates with exogenous orienting under greater temporo-parietal and ventral frontal cortex control while the posterior parietal and frontal cortex play a stronger role in endogenous orienting (Muller and Rabbitt, 1989; Rafal et al., 1989; Rafal and Henik, 1994; Deubel, 1995; Corbetta and Shulman, 2002; Mayer et al., 2004; Mort et al., 2003; Grosbras et al., 2005; although see Peelen et al., 2004 who observed no differences in neural activity using an fMRI based approach). Either of these two attentional mechanisms can occur with (overt orienting) or without (covert orienting) an accompanying eye movement. It remains unclear as to whether covert shifts of attention can occur independently of oculomotor planning (independence hypothesis) or whether they actually represent oculomotor programming (identity hypothesis). The former view is encapsulated in the spotlight metaphor of attention (Posner et al., 1980) while the latter view is expressed in the oculomotor readiness hypothesis (Klein, 1980) or the premotor theory (Rizzolatti et al., 1987) which both emphasize that covert orienting of attention is the same as preparing to make an overt eye movement to look at that location.

A vast effort has been devoted to disentangling this issue and it would appear that an intermediate stance whereby the two systems share resources at some stage (interdependence hypothesis) appears most likely (for a review see Awh et al., 2006). Evidence indicates that it is not possible to make an eye movement without a prior shift in attention to the desired location (Shepherd et al., 1986) and that attention directed towards a target both facilitates saccades and enhances perceptual identification at the saccade goal (Kowler et al., 1995). Nevertheless, once saccade programming is complete some attention can be diverted from the saccade goal with little cost to the saccade latency or accuracy (Kowler et al., 1995). More recently, imaging studies have strengthened evidence for overlapping neural areas involved in covert and

overt attention orienting (Corbetta, 1998; Nobre et al., 2000; Grosbras et al., 2005). However, evidence at the single cell level suggests that any dissociation may only be apparent on a finer scale (Sato and Schall, 2003; Ignashchenkova et al., 2004; Thompson et al., 2005) and that task differences may recruit the two systems to differing degrees (Theeuwes et al., 1998; Abrams and Pratt, 2000; Tse et al., 2002; Hunt and Kingstone, 2003; Sumner et al., 2004). Observations of a relationship between microsaccades and covert attention shifts support the view that eye movement programming occurs during covert attention shifts (Hafed and Clark, 2002; Engbert and Kliegl, 2003a; Rolfs et al., 2004; Laubrock et al., 2005), although such a trend remains to be demonstrated in SI.

A common paradigm used to investigate the effects of exogenous and endogenous attention is the cue–target task (Posner, 1980; Posner and Cohen, 1984). During the exogenous form of the task, a non-informative peripheral cue is briefly presented (usually at one of two locations), whereas during the endogenous condition, a central symbolic cue is presented indicating which location is the most likely location for the target. Following either type of cue, a target is presented at the cued or uncued location. Manual and saccadic responses to the target exhibit distinct patterns of facilitation or inhibition depending on the cue type. In the case of exogenous cueing, latencies are faster (facilitation) if the target is presented at the cued location less than 200 ms following the cue, but are longer if the target is presented over 300 ms later (Klein, 2000). This late inhibitory effect is termed inhibition of return (IOR) and can last for up to 3 s (Posner and Cohen, 1984; Posner et al., 1985). With endogenous cueing, facilitation towards the cue occurs later (from approximately 150 ms) and IOR is absent during manual response conditions unless the cue triggers a saccade to be prepared or executed (Muller and Rabbitt, 1989; Rafal et al., 1989; Fecteau et al., 2004).

### 1.3. Attention and microsaccades

Recent work employing such a cue–target task has demonstrated that microsaccade direction and frequency are affected by exogenous and endogenous attention shifts (Hafed and Clark, 2002; Engbert and Kliegl, 2003a; Rolfs et al., 2004; Laubrock et al., 2005). During both exogenous and endogenous cuing, microsaccade frequency first decreases then increases to a maximum approximately 400 ms following the cue. In contrast, microsaccade direction is affected differently between the two attention conditions: approximately 200 ms following the exogenous cue, microsaccades tend to be directed away from the cue, whereas during endogenous cuing this effect is absent or reversed. Previous authors (Engbert, 2006; Hafed and Clark, 2002; Laubrock et al., 2005; Rolfs et al., 2005) have speculated that microsaccades may be a consequence of exogenous and endogenous influence on the superior colliculus (SC) build up cells. The SC controls saccadic initiation, amplitude and direction through mutually inhibitory connections between rostral and caudal build up cells (Munoz and Wurtz, 1992, 1993a,b, 1995a,b; Munoz and Istvan, 1998; Krauzlis et al., 2000). The rostral build up cells (also known as fixation cells) represent the foveal region of the visual field and are active during fixation when they suppress larger saccades through

inhibition of the caudal build up cells. Activity within these rostral build up cells is also associated with small saccades in the amplitude range of microsaccades and SI (Munoz and Wurtz, 1993a). Consequently the level and location of activity within these rostral build up cells may dictate microsaccade frequency and direction.

SI and microsaccades may represent essentially alternate descriptions for the same underlying phenomena. Early reports differentiated microsaccades from SI on the basis of their smaller amplitude, higher frequency and absence of a return saccade (Steinman et al., 1967, 1973; Ditchburn, 1980; Herishanu and Sharpe, 1981; Steinman et al., 1982; Carpenter, 1988; Shallo-Hoffmann et al., 1989, 1990; Kowler, 1991; Abadi and Gowen, 2004). However, these differences can be explained by arbitrary classification techniques. For example, early SI studies employed low-resolution recording techniques ( $>0.5^\circ$ ) which would have been insufficient to detect smaller microsaccades and may have led to the belief that SI were larger. Together with the fact that both SI and microsaccade research have employed overlapping amplitude criteria this makes any distinction based on amplitude tenuous. Indeed, Hafed and Clark (2002) noted that division of microsaccades into those above and below  $0.5^\circ$  did not affect the relationship between attention and microsaccades. The reported higher frequency of microsaccades may also be accounted for by lower resolution recording techniques and/or different data analysis techniques: in microsaccade studies, the second return saccade is counted as a separate microsaccade, whereas during SI analysis, the return saccade is considered part of one SI. In addition, more recent findings indicate that both microsaccades and SI are mainly of a horizontal nature (Abadi and Gowen, 2004; Engbert and Kliegl, 2003b; Engbert, 2006). Evidence that attention and task instructions exert similar effects on both (Barlow, 1952; Steinman et al., 1967, 1973; Winterson and Collewijn, 1976; Kowler and Steinman, 1980; Gowen et al., 2005) and that microsaccades and SI share characteristics such as inter-saccade duration (Feldon and Langston, 1977; Ohtsuka et al., 1986) also suggests that they are closely related. If modulation of SI frequency and direction by exogenous and endogenous attention was found to resemble that for microsaccades, this would support the argument for a close association.

Consequently, we wished to explore whether SI characteristics such as amplitude, frequency and direction would also be influenced by exogenous or endogenous changes in attention. Therefore, as a more rigorous test of the preliminary study by Gowen et al. (2005), we investigated the effect of both exogenous and endogenous cuing on SI characteristics in 12 subjects. Our aims were threefold. Firstly, we wished to examine whether exogenous and endogenous attention have differential effects on SI. Secondly, we aimed to discover whether exogenous and endogenous attention shifts would affect SI in a similar manner to microsaccades, which would provide evidence that the two forms of eye movement are linked. Specifically, whether SI are directed away from the cue during the exogenous condition, but towards the cue during endogenous conditions. Thirdly, earlier findings hinted that SI characteristics were influenced differently depending on the response mode; SI amplitude was larger and SI frequency lower during saccadic as opposed to manual trials (Gowen et

al., 2005). Differences between saccadic and manual IOR have been observed previously (Abrams and Pratt, 2000; Hunt and Kingstone, 2003; Sumner et al., 2004) and any differential effect on SI would support a decoupling between covert attention orienting and eye movement planning.

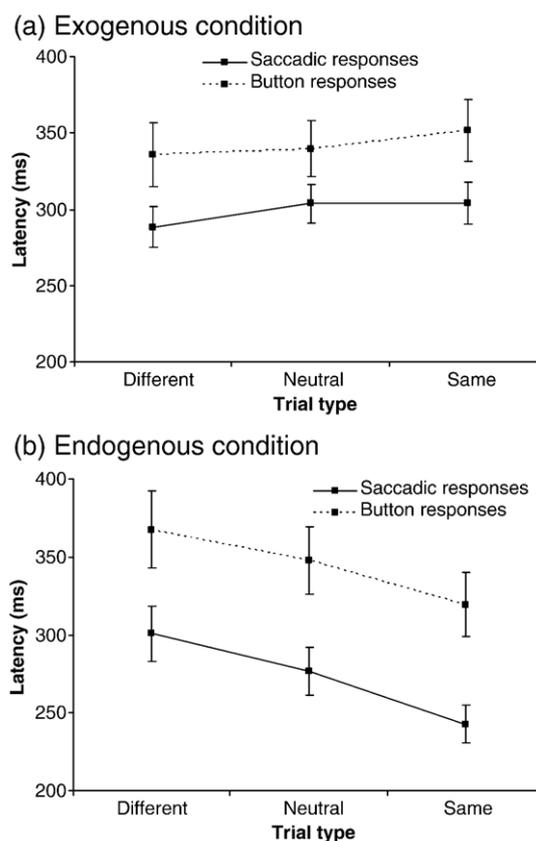
## 2. Results

### 2.1. SI characteristics

Results from the control primary position fixation task revealed that mean ( $\pm$ standard deviation) SI amplitude and frequency were  $0.54 \pm 0.26^\circ$  and  $18.66 \pm 12.86$  per minute respectively. Mean SI directional bias (percent of SI directed to the right) was  $63.9\% \pm 23.51$ . These characteristics are consistent with those previously reported in a healthy population (Abadi and Gowen, 2004).

### 2.2. Response latencies

Mean reaction times for the exogenous and endogenous conditions can be seen in Figs. 1a and b respectively. A  $2 \times 3 \times 2$  within-factor ANOVA with factors of attention condition (exogenous/endogenous), cue type (same/neutral/different) and response mode (button press/saccade) revealed a



**Fig. 1 – Saccade latencies (continuous line) and manual latencies (dashed line) over the different trial types for (a) exogenous cuing condition and (b) endogenous cuing condition. Standard error bars are shown.**

significant effect of cue type ( $F(2,22)=5.09$ ,  $p=0.015$ ) and response mode ( $F(1,11)=16.1$ ,  $p=0.002$ ) but no significant main effect of attention condition ( $F(1,11)=2.19$ ,  $p=0.17$ ). The interaction between attention condition and cue type was significant ( $F(2,22)=34.28$ ,  $p<0.0001$ ); all other interactions were not significant. Although there was a trend for subjects to respond faster to the different cue types during the exogenous condition, follow-up paired  $t$  tests with a corrected  $\alpha$  of 0.004 revealed that there was no significant difference between same and different cues for the exogenous saccadic ( $t=-1.74$ ,  $p=0.11$ ) or exogenous manual ( $t=-2.19$ ,  $p=0.05$ ) task. There was, however, a significant difference between same and different cues types for the endogenous saccadic ( $t=4.82$ ,  $p=0.001$ ) and endogenous manual ( $t=3.58$ ,  $p=0.004$ ) tasks. These results indicate that our experimental conditions produced different effects on response times that were dependent on attention condition. That is during exogenous conditions there was a trend for subjects to respond more slowly when the target direction was the same as the preceding cue direction (IOR) whereas during endogenous conditions, subjects were significantly faster to respond when the target direction was the same as the preceding cue. Finally, manual responses were slower than saccadic responses during both attention conditions.

### 2.3. The effect of trial time on SI characteristics

In order to document any changes in SI behaviour over the course of a trial and to enable us to compare these findings with our previous work (Gowen et al., 2005), SI amplitude, frequency and percent to cue were analysed separately across different trial periods (Before trial/Central target to cue/Cue to target/Target to end) in the different experimental conditions (Section 2.3.1). Planned comparisons of the SI features during the critical cue–target interval were also undertaken (Section 4.4.2). In the following analysis, parametric statistics have been employed for the analysis of SI amplitude and SI% to cue and non-parametric statistics (Friedman's, Wilcoxon signed ranks test) for SI frequency (see Experimental procedures section). A Bonferroni adjustment to a corrected level of  $\alpha=0.01$  was employed for all non-parametric statistics.

#### 2.3.1. SI characteristics across different trial periods

**2.3.1.1. SI amplitude.** A  $2 \times 2 \times 3 \times 4$  within-factor ANOVA with factors of attention condition (exogenous/endogenous), response mode (button press/saccade), cue type (same/different/neutral) and trial period revealed no significant effects of attention condition ( $F(1,10)=0.006$ ,  $p=0.939$ ), response mode ( $F(1,10)=3.34$ ,  $p=0.1$ ) or trial type ( $F(2,20)=0.174$ ,  $p=0.842$ ) but that SI amplitude significantly varied across the trial periods ( $F(3,30)=16$ ,  $p<0.001$ ). This can be observed in Fig. 2a where SI amplitudes are larger at the beginning and end of a trial compared with the centre portion. Paired  $t$  tests revealed significant differences between all trial periods ( $t \geq 3.73$ ,  $p \leq 0.001$ ), except between the central target to cue and the cue–target periods ( $t=1.29$ ,  $p=0.28$ ). No significant interactions were observed ( $F \leq 2.08$ ,  $p \geq 0.12$ ). Therefore, SI amplitude was similar under all task conditions and only varied during the different trial periods.

**2.3.1.2. SI frequency.** Fig. 2b displays SI frequency characteristics for exogenous and endogenous conditions. A Friedman's test revealed that SI frequency did not significantly differ between exogenous and endogenous trial conditions ( $\chi^2=0.5$ ,  $p=0.48$ ) or between response modes ( $\chi^2=1.13$ ,  $p=0.29$ ). No significant interactions were observed between attention condition and response mode (exogenous versus endogenous manual trials,  $z=-0.16$ ,  $p=0.87$ ; exogenous versus endogenous saccadic trials,  $z=-2.1$ ,  $p=0.04$ ; corrected  $\alpha=0.01$ ).

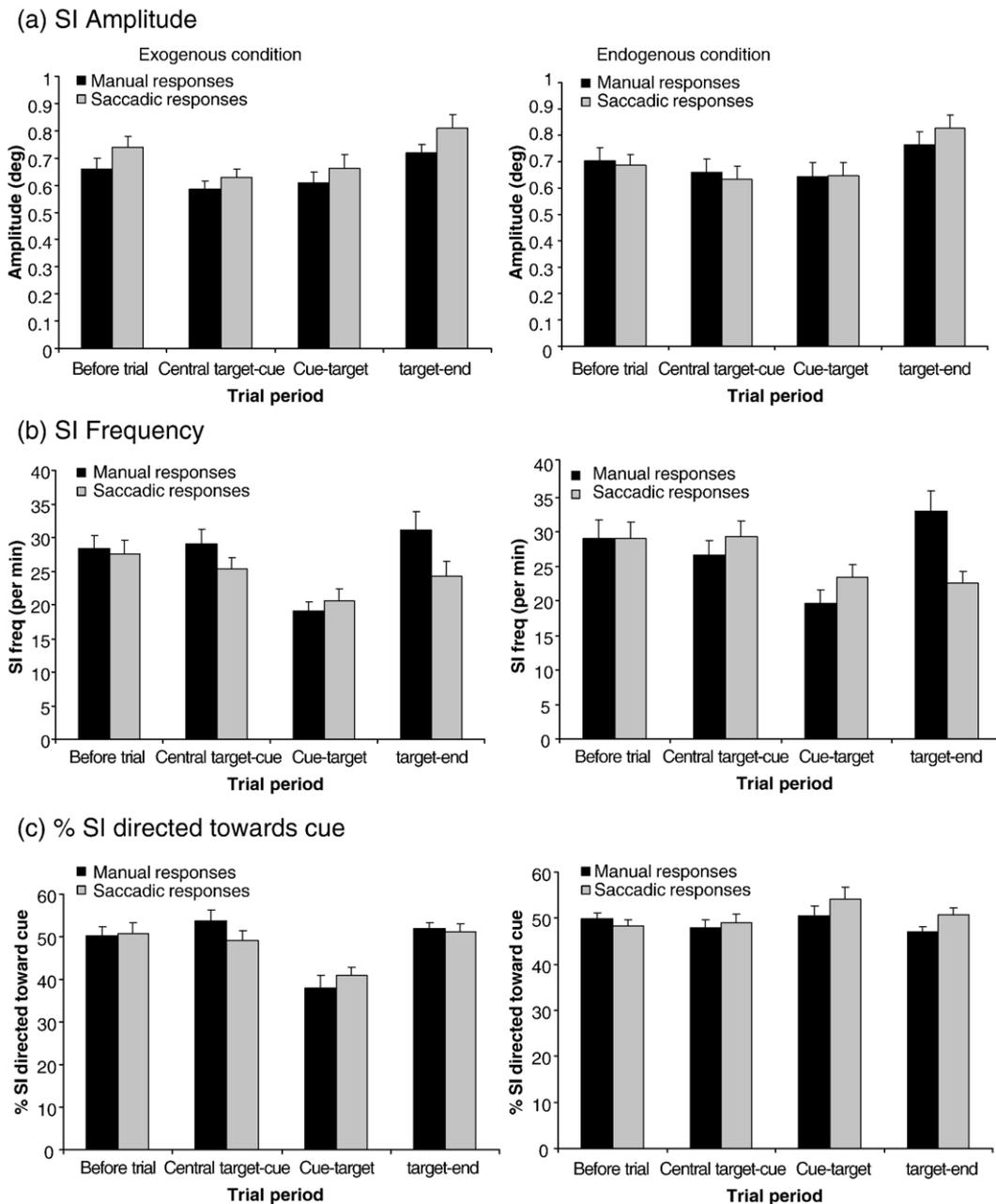
Comparison of SI frequency across trial periods revealed significant differences ( $\chi^2=59.48$ ,  $p<0.001$ ). This was the case for both attention conditions ( $\chi^2 \geq 13.23$ ,  $p \leq 0.004$ ) and for each response mode ( $\chi^2 \geq 26.42$ ,  $p \leq 0.001$ ). A Wilcoxon test across all trial conditions indicated that SI frequency was significantly lower during the cue–target period than all other periods ( $z \geq -5.96$ ,  $p < 0.005$ ). Saccadic response mode was compared to manual response mode for each trial period. For the exogenous condition, SI frequency was significantly higher for manual responses (33.75 per second) as opposed to saccadic responses (23.6 per second) during the target appearance–end period only ( $z=-3.11$ ,  $p<0.0021$ ) but for the endogenous conditions there were no differences between the response modes for any trial period ( $z \leq 2.23$ ,  $p \geq 0.03$ ; corrected  $\alpha=0.01$ ).

SI frequency was significantly affected by cue type ( $\chi^2=10.8$ ,  $p=0.006$ ; same=26.49 per minute; different=26.71 per minute; neutral=25.1 per minute; Table 1). This was not significant over the different attention conditions ( $\chi^2 \leq 6.3$ ,  $p \geq 0.04$ ; corrected  $\alpha=0.01$ ) or the different response modes ( $\chi^2 \leq 5.44$ ,  $p \geq 0.07$ ). However, when cue type was analysed against trial period, SI frequency was significantly lower for neutral trials during the target–end period ( $\chi^2=17.37$ ,  $p<0.001$ ; same=28.98 per minute; different=28.54 per minute; neutral=25.6 per minute).

In summary, SI frequency did not differ across the attention conditions, response mode or cue type but was significantly lower during the cue–target interval (i.e., SOA of 1200 ms) for all these conditions. Furthermore, SI frequency was higher for manual responses during the target appearance–end period, particularly during the exogenous condition and appeared to be lower for neutral trials during this period.

**2.3.1.3. SI direction.** Neutral trials were analysed separately as the outcome parameter (%rightward) differs from directional cue trials (percent to cue). A  $2 \times 2 \times 4$  repeated measures ANOVA with factors of attention condition (exogenous/endogenous), response mode (manual/saccadic) and trial period revealed no significant effects of attention condition, response mode or trial interval ( $F \leq 1.89$ ,  $p \geq 0.16$ ). However, there was a significant interaction between attention condition and trial period ( $F(3,69)=8.18$ ,  $p=0.001$ ). A paired sampled  $t$  test indicated that there was a higher percentage of SI directed towards the cue in the endogenous condition compared to the exogenous condition only for the cue–target period (exogenous=39.42%, endogenous=52.35%,  $t=-4.11$ ,  $p<0.0005$ ). This can be observed in Fig 2c.

A second repeated measures ANOVA with the same factors as above examined the pattern of rightward directed SI in the neutral trials over the different conditions. There



**Fig. 2 – SI amplitude (a), frequency (b) and percent of SI directed towards the cue (c) for manual (black bars) and saccadic (grey bars) responses over the four different trial periods. Exogenous and endogenous conditions are shown on the left and right respectively. Cue types (same/different/neutral) are combined. Standard error bars are shown.**

was no effect of attention condition, response mode or trial period ( $F \leq 1.1$ ,  $p \geq 0.32$ ) and crucially no interaction between attention condition and trial period ( $F(3,33) = 1.4$ ,  $p = 0.26$ ).

In summary, the percent of SI directed towards the cue tended to be lower during the cue-target period in the exogenous condition compared to the endogenous condition. However, there was no effect of experimental conditions on the rightward bias in the neutral trials. In order to examine this effect in more detail we next analysed SI characteristics during the cue-target period only.

### 2.3.2. SI characteristics during cue-target period

SI characteristics were investigated across the cue-target interval separated in  $12 \times 100$  ms bins (see Experimental procedures section (SI analysis) for details).

**2.3.2.1. SI amplitude.** These group results can be seen in Figs. 3a–b. As data were missing from some time windows (where no SI had occurred for certain subjects), amplitude averages for each condition were collapsed across three bins (300-ms time windows) giving a total of four time windows. These were submitted to a  $4 \times 2 \times 2$  repeated measures ANOVA

**Table 1 – SI frequency during each trial period for cues that were in the same or different direction as the target or were neutral in respect to the target direction**

Trial period	SI frequency (per min) for each cue type		
	Same	Different	Neutral
Before trial	28.35	29.05	28.04
CC-Cue	28.04	27.72	26.9
Cue-target	20.04	21.51	19.85
Target-end	28.98	28.54	25.6

Both attention conditions and response modes have been combined.

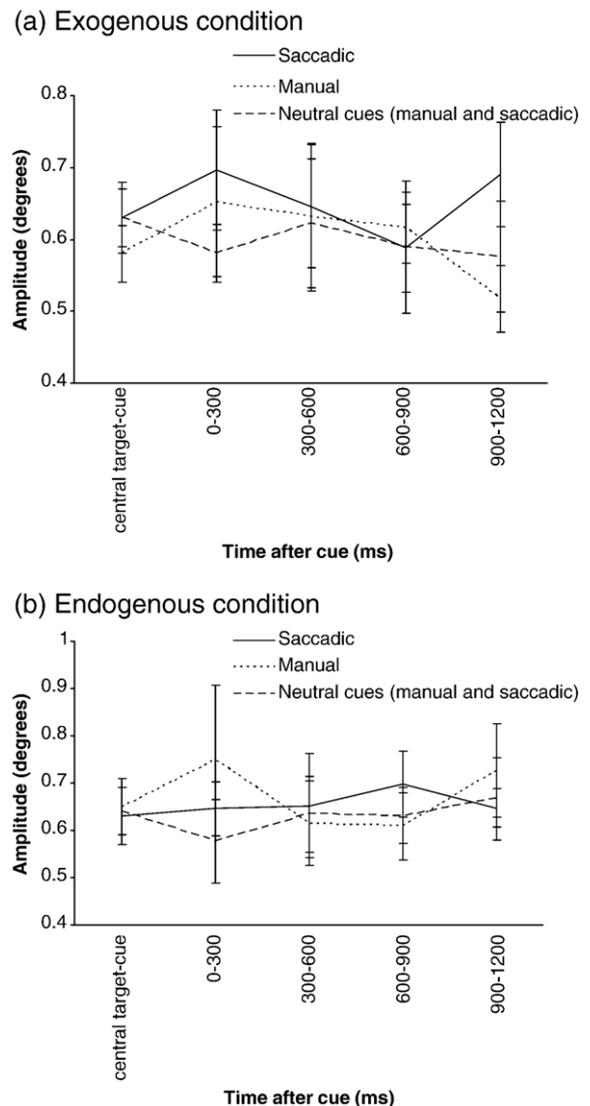
with factors of time window, attention condition (exogenous/endogenous) and response mode (manual/saccadic). There was a significant main effect of response mode ( $F(1,10)=6.02, p=0.02$ ) indicating that SI amplitude was higher for saccade trials and a significant three-way interaction ( $F(3,30)=4.65, p=0.01$ ) which was further analysed using two separate repeated measures ANOVAs for each response type with factors of attention condition (exogenous/endogenous) and time window. For the saccade response mode there was only a main effect of time window ( $F(3,30)=3.44, p=0.03$ ), whereas for the manual response condition there was an interaction between attention condition and time ( $F(3,33)=3.35, p=0.03$ ). SI amplitude was higher in the endogenous manual condition compared to the exogenous manual condition, but only during the last time window following the cue ( $t=2.8, p=0.02$ ; corrected  $\alpha=0.01$ ), whereas SI amplitude did not vary between the exogenous and endogenous saccadic conditions.

Because there were fewer neutral trials, we had insufficient numbers of SI to perform the above analysis so the averages across each time window during the cue-target period were collapsed for all subjects and submitted to a  $2 \times 2 \times 2$  repeated measures ANOVA with factors of cue type (neutral or informative cue) attention condition (exogenous or endogenous) and response type (manual or saccadic). There was a significant effect of cue type ( $F(1,11)=12.76, p=0.004$ ) but no significant effect of attention ( $F(1,11)=2.09, p=0.18$ ) or response mode ( $F(1,11)=3.66, p=0.08$ ) and no significant interactions ( $F(1,11) \leq 0.49, p \geq 0.5$ ). It can be observed in Figs. 3a–b that although SI amplitude modulation across the different time periods appears similar in both neutral and informative cue trials, SI amplitude in neutral trials was significantly smaller.

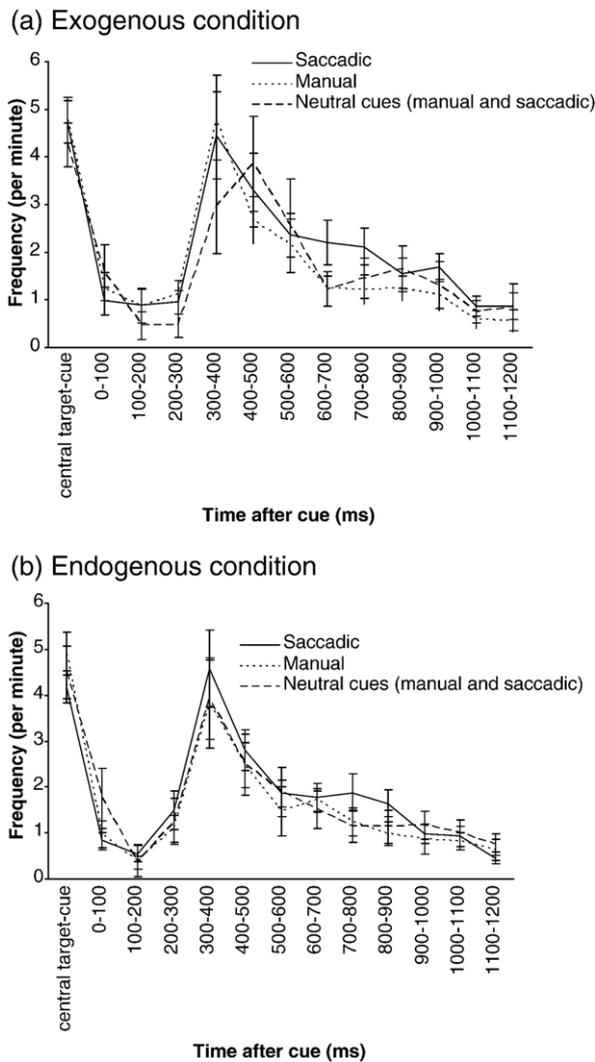
**2.3.2.2. SI frequency.** SI frequency changes over the different time windows can be seen in Figs. 4a–b. Friedman testing revealed that SI frequency differences were highly significant across the twelve time windows, for all task conditions ( $\chi^2 \geq 44.07, p \leq 0.0005$ ). There was no significant difference between exogenous or endogenous conditions ( $z=-1.39, p=0.17$ ), but the frequency was significantly higher for saccadic (1.75 per minute) compared to manual (1.47 per minute) responses ( $z=-3.49, p < 0.0005$ ). In the neutral cue conditions, there was a significant effect of time for all conditions ( $\chi^2 \geq 23.77, p \leq 0.01$ ) but there was no difference between exogenous or endogenous conditions ( $z=-0.35, p=0.73$ ) or between saccadic and manual response mode ( $z=-0.86, p=0.39$ ).

In summary for both attention conditions, response modes and all cue types, SI frequency tended to decrease to a minimum following the cue onset, then rise to reach a peak at approximately 300–400 ms post cue before slowly returning to minimum levels by 1200 ms after the cue. SI frequency during saccadic response trials was higher than manual trials. During neutral cue trials, SI frequency followed a similar pattern for all attention conditions and response modes, although there was a non-significant tendency for frequency to be lower than directional cues and a trends for the pattern to occur later during the exogenous condition.

**2.3.2.3. SI direction.** In order to statistically examine how trial conditions affected SI direction, the number of SI directed



**Fig. 3 – SI amplitude over the different time windows during the cue-target interval for the exogenous (a) and endogenous (b) conditions. Central target-cue = average SI amplitude over the preceding trial period (central target illumination-cue). Manual trials are denoted by the continuous line, saccadic trials by the dotted line and combined manual and saccadic neutral trials by the dashed line. Standard error bars are shown.**

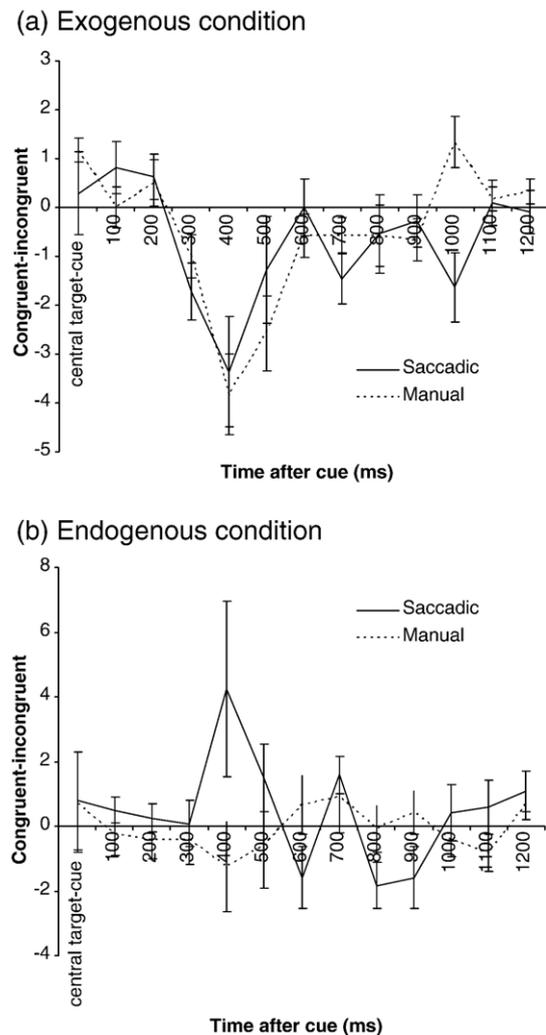


**Fig. 4 – SI frequency over the different time windows during the cue–target interval for the exogenous (a) and endogenous (b) conditions. Central target–cue=average SI frequency over the preceding trial period (central target illumination–cue). Manual trials are denoted by the continuous line, saccadic trials by the dotted line and combined manual and saccadic neutral trials by the dashed line. The CC–cue interval represents the average frequency during any 100-ms window during the central cue–cue interval. Standard error bars are shown.**

towards the cue (congruent) was subtracted from the number of SI in the opposite direction to the cue (incongruent) (Laubrock et al., 2005). Zero indicates that an equal number of SI were directed towards and away from the cue, positive values indicate a higher frequency of SI directed towards the cue and negative values indicate a higher frequency of SI directed away from the cue (Figs. 5a–b). These bias values were submitted to a repeated measures ANOVA with factors of time, response mode (manual/saccadic) and attention condition (exogenous/endogenous). This revealed a main effect of attention condition ( $F(1,11)=5.45, p=0.04$ ), but no main effect of time ( $F(11,121)=1.41, p=0.25$ ) or response mode ( $F(1,11)=0.61, p=0.45$ ). There was a significant interaction between

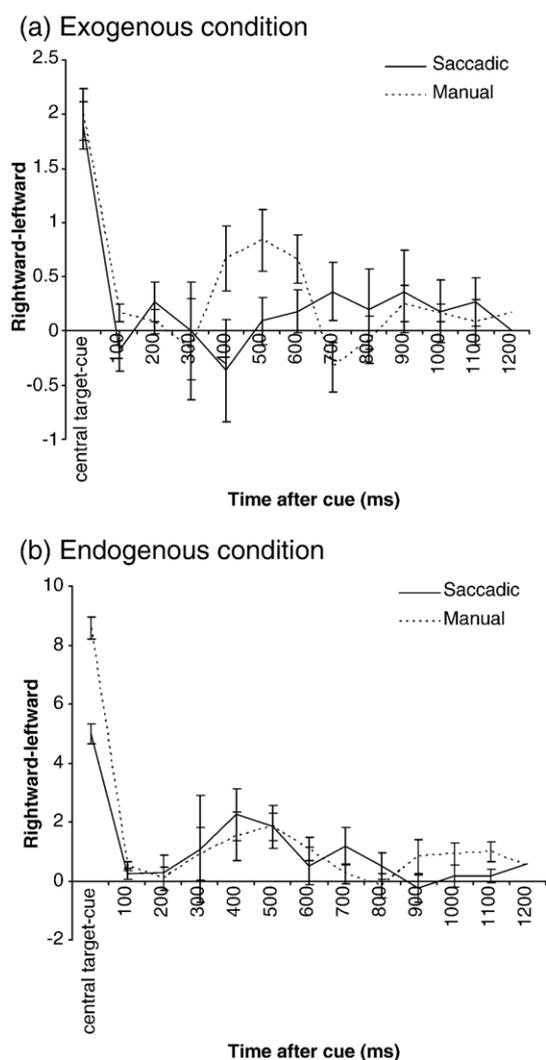
attention condition and time ( $F(11,121)=3.35, p=0.03$ ) and response mode and time ( $F(11,121)=2.93, p=0.02$ ) and a significant three-way interaction between attention condition, response mode and time ( $F(11,121)=2.62, p=0.05$ ). No significant interaction was observed between response mode and attention condition ( $F(1,11)=2.0, p=0.19$ ).

Post hoc paired *t* tests (corrected  $\alpha=0.01$ ) indicated that the attention×time interaction was due to a greater number of congruent SI in the endogenous compared to the exogenous condition 400 ms ( $t=-2.66, p=0.01$ ) and 700 ms ( $t=-4.21, p=0.005$ ) following the cue. The response×time interaction was due to more incongruent SI in the manual response condition 400 ms following the cue which was not significant using the adjusted  $\alpha$  ( $t=-2.27, p=0.03$ ). The three-way



**Fig. 5 – The number of congruent SI subtracted from the number of incongruent SI over the different time windows during the cue–target interval for the exogenous (a) and endogenous (b) conditions. Positive values indicate a larger number of congruent SI, negative values indicate a larger number of incongruent SI. Central target–cue=average SI direction over the preceding trial period (central target illumination–cue). Manual trials are denoted by the continuous line, and saccadic trials by the dotted line. Standard error bars are shown.**

interaction was analysed for exogenous and endogenous conditions using 2 separate ANOVAs with factors of response mode and time interval. Both conditions showed an interaction between response mode and time interval ( $F(11,121) \geq 2.14$ ,  $p \leq 0.02$ ). For the exogenous condition there were more incongruent SI during the saccadic response mode 1000 ms following the cue ( $t = -3.48$ ,  $p = 0.005$ ). However, for the endogenous condition there were more congruent SI during the saccadic condition 400 and 800 ms following the cue. These results are shown in Figs. 5a–b. In short, during exogenous conditions, approximately 400 ms following the cue, SI tended to be directed away from the cue whereas during endogenous conditions SI direction remained stable (manual condition) or were directed towards the cue (saccadic condition).



**Fig. 6** – The number of rightward SI subtracted from the number of leftward SI over the different time windows following a neutral cue for the exogenous (a) and endogenous (b) conditions. Positive values indicate a larger number of rightward SI, negative values indicate a larger number of leftward SI. Central target–cue = average SI direction over the preceding trial period (central target illumination–cue). Manual trials are denoted by the continuous line, and saccadic trials by the dotted line. Standard error bars are shown.

A second repeated measures ANOVA with factors of time, response mode (manual/saccadic) and attention condition (exogenous/endogenous) compared the number of SI directed rightward with those directed leftward for neutral cues. This revealed no significant effect of attention condition ( $F(1,9) = 3.27$ ,  $p = 0.1$ ), or an interaction between attention condition and time ( $F(11,99) = 0.47$ ,  $p = 0.92$ ), indicating that SI direction was only biased differently in the exogenous and endogenous conditions when a directional cue was presented (Figs. 6a–b). Figs. 6a–b also show that following the neutral cue the usual rightward SI bias is reduced

### 3. Discussion

We have examined the effect of exogenous and endogenous attention orienting on SI through the use of a cue–target paradigm and our work provides three main findings: (1) SI characteristics are influenced by both exogenous and endogenous attention orienting; (2) SI responses to exogenous and endogenous cues resemble previously published microsaccade behaviour; and (3) SI characteristics during the endogenous cue–target interval are dependent on the response mode. We will first address how SI are affected by attention and in what ways this replicates previous microsaccade findings, followed by how our results extend this previous work in regards to response mode.

#### 3.1. The influence of exogenous and endogenous attention on SI characteristics

When examining SI across a ~5-s trial, a similar pattern in the modulation of SI amplitude and frequency occurred regardless of attention condition or response mode. SI amplitude was largest during the before trial and trial end periods and SI frequency lowest during the cue–target interval. These results can be explained by the requirement to maintain the eyes at a central location while having to respond to the peripheral cue and are in agreement with Gowen et al. (2005) who found that increased endogenous attention to a central fixation target leads to decreased SI frequency and amplitude. The observation that SI frequency was lower for neutral cues than directional cues (for both attention conditions and response modes), particularly during the target–end interval, suggests that the prior modulation by a directional cue affects post response SI. Perhaps the onset of simultaneous bilateral cues during the exogenous neutral cue condition and the absence of expectation during the endogenous neutral cue task provoke greater suppression of SI. The effect of two peripheral cues on SI frequency is explored in more detail later.

In regards to SI characteristics during the cue–target interval, our data have replicated previous behavioural findings for microsaccades showing that frequency and direction are influenced by both exogenous and endogenous attention (Hafed and Clark, 2002; Engbert and Kliegl, 2003a; Galfano et al., 2004; Rolfs et al., 2004; Laubrock et al., 2005). Early exogenous orienting to the cue onset may have caused the initial frequency decrease. This is most likely an automatic response to stimulus change, rather than due to attention shifts as this was observed with both peripheral and central

cues and directional and neutral cues. Indeed, irrelevant visual stimuli produce similar decreases in microsaccade frequency (Engbert and Kliegl, 2003a) and in larger voluntary saccades (Reingold and Stampe, 2002, 2004) and it has been suggested that this early inhibition arises from direct retinotectal input (Engbert, 2006). Unlike voluntary saccades where exogenous facilitation occurs during the first 100 ms post cue, SI did not appear to be preferentially directed towards the cue. This has also been observed with microsaccades (Galfano et al., 2004; Rolfs et al., 2004) and may be due to the small amount of data collected during this low-frequency period or the requirement to ignore the cue and maintain fixation. The time when SI were at their maximum frequency corresponded with a change in SI direction where SI were predominantly directed away from the cue during the exogenous task (resembling IOR; Klein, 2000) or towards the cue during the endogenous saccadic task (resembling endogenous facilitation; Muller and Rabbitt, 1989). This increase in SI frequency during the change in SI direction suggests that shifting attention (towards the cued location in the endogenous task and away from the cued location in the exogenous task) leads to a release of SI and that the processes controlling spatial attention and fixation are similar. However, the time (approximately 600 ms) at which SI frequency and direction for all conditions reach equilibrium, is much earlier than IOR or facilitation usually disappears (Posner and Cohen, 1984; Toassinari et al., 1987; Muller and Rabbitt, 1989). This suggests that at this point, voluntary attentional mechanisms that are separate from IOR or endogenous facilitation and perhaps due to the fixation demands of the task prevent further influence of IOR or facilitation on SI. Laubrock et al. (2005) also proposed the existence of two endogenous processes: one related to attention shifting and one related to task instruction. The fact that both microsaccade amplitude in their study and SI amplitude in ours were unaffected by task conditions highlights the strong hold of fixation on ocular alignment. On the other hand, processing demands related to IOR and endogenous attention may diminish, enabling greater resources to be available for fixation control. Alternatively, SI may be more sensitive to shifts in attention rather than maintaining attention at one location.

### 3.2. *The relationship between microsaccades and SI*

Historically, a saccade during fixation has been considered to either represent a microsaccade or a SI and with few exceptions (Feldon and Langston, 1977; Hafed and Clark, 2002; Ohtsuka et al., 1986) they have not been referred to in the same context. The above similarities between microsaccades and SI support the conjecture that the two saccadic behaviours relate to the same phenomena. This is also suggested by previous findings that they are both of an involuntary nature, adhere to the main sequence, are predominantly conjugate and observed in the horizontal plane and display a decreased frequency when attention levels are raised (Barlow, 1952; Kowler and Steinman, 1980; Steinman, 1965; Steinman et al., 1967; Møller et al., 2002; Engbert and Kliegl, 2003a,b; Engbert, 2006; Abadi and Gowen, 2004; see Martínez-Conde et al., 2004 for a review) In contrast to our upper amplitude limit of 4°, previous microsaccade research has employed a cut-off of 1°. However, we would hesitate to

suggest that we have replicated findings in a larger saccade group as only 2% of SI were above 1°, which also emphasises that for both SI and microsaccades the upper amplitude range is highly comparable. For the same reason, it is important to state that our data do not reflect larger voluntary eye movements.

Although our SI frequency as well as those previously reported (Herishanu and Sharpe, 1981; Ohtsuka et al., 1986; Shallo-Hoffmann et al., 1989, 1990; Abadi and Gowen, 2004) is substantially lower than the mean microsaccade frequency of 1–2 per second (Ditchburn, 1980; Steinman et al., 1982; Carpenter, 1988a; Kowler, 1991; Engbert and Kliegl, 2003a) this may be accounted for by the fact that microsaccade studies include both initial and return components and tend to use recording techniques with higher temporal and spatial resolution (240–500 Hz, 0.01–0.06° as opposed to our 200 Hz, 0.09°) (Hafed and Clark, 2002; Engbert and Kliegl, 2003a; Laubrock et al., 2005). Furthermore, our threshold for saccade detection was 20°/s which would not have detected very small SI (<0.15°). One feature that apparently distinguishes SI and microsaccades is the presence of a return saccade in the former. In order to explain this potential difference, two possibilities present themselves. Firstly, microsaccades frequently do present as coupled (Ohtsuka et al., 1986; Hafed and Clark, 2002) but the second saccade is not included in the analysis. Secondly, the classification of microsaccades as single sided stems from early research which also classified their amplitude as ~0.15° (Ditchburn, 1980; Steinman et al., 1982; Carpenter, 1988a; Kowler, 1991). As visual resolution decreases when the retinal image leaves the central 0.3° of the fovea (Steinman et al., 1973, 1982; Westheimer and McKee, 1975) and microsaccade amplitude in the above range does not frequently exceed this area, error detection and correction and a return saccade may have occurred less frequently. Indeed, coupling of microsaccades has been reported when their amplitude is larger (Ditchburn and Ginsborg, 1953; Hafed and Clark, 2002).

A further issue that requires comment is that of SI/microsaccade conjugacy and movement direction. Recent evidence has suggested that although microsaccades are predominantly conjugate and of a horizontal nature, they not uncommonly exhibit vertical monocular characteristics (Engbert and Kliegl, 2003b; Engbert, 2006). At first glance this appears at odds with our previous work demonstrating that SI mainly occur as a horizontal and conjugate phenomena; we found evidence for conjugate horizontal or oblique SI only (Abadi and Gowen, 2004). However, with this exception, much of our work (Gowen and Abadi, 2005; Gowen et al., 2005) has been conducted using horizontal eye movement trackers so if it is the monocular microsaccades that are mainly of a vertical nature we would not have observed either the vertical or monocular component.

Therefore, our results support the theory that the terms “microsaccade” and “SI” may essentially represent different names given to the same type of fixational eye movement. Indeed it may seem more appropriate to employ a generic term such as “fixation saccade” to include both terms. In order to further strengthen this argument future studies using high-resolution, binocular, 3D recording systems together with a consistent detection algorithm for both microsaccades and SI should aim to uncover whether vertical

monocular SI occur and whether microsaccades and SI display a correlation between size and coupling. Our data are unable to directly contribute towards this latter question as only 8% of the SI were classified as single sided. However, this does infer that smaller amplitude SI, in the range below our detection criterion may be more frequently of the single sided type. Finally, recent evidence indicates that microsaccade production is determined by retinal slip velocity (Engbert and Mergenthaler, 2006) which provides additional avenues down which to draw behavioural parallels.

### 3.3. *The relationship between attention and eye movements: what can SI contribute?*

Our findings indicate that the degree to which attention and oculomotor control overlap during a particular task may also be apparent in changes SI behaviour. Across exogenous and endogenous conditions SI amplitude and frequency were higher for the saccadic response mode during the cue–target interval, suggesting that saccade planning may influence SI frequency. SI frequency was higher for manual responses during the target appearance–end period, indicating that either attention may have been diverted from maintaining steady fixation to responding in a different modality or that making a saccade allowed less opportunity for SI to occur. A further difference between the response modes occurred during endogenous conditions, when SI direction was biased towards the cue in the saccadic but not manual trials. Reaction times were shorter in the valid cue conditions compared to the invalid type for both manual and saccadic response trials indicating that subjects were using the cues appropriately. We cannot discount that spatial preparation of the saccadic response may have had greater influence on SI direction than non-spatially dependent manual responses (Simon, 1990). However, even if this were to be the case, our findings still suggest a dissociation between attention and saccade processing. Our results appear in contrast to Engbert and Kliegl (2003a) who observed an increase in cue congruent microsaccades during both endogenous saccadic and manual response trials. However, they used symbolic arrow cues that cause stronger congruency effects and are known to involve involuntary attentional orienting (Gibson and Bryant, 2005). Furthermore, there is suggestion that when saccade preparation to an endogenous cue is not required, microsaccade direction is not oriented towards the cue (Laubrock et al., 2005). Therefore, it is likely that if the same task using colour cues was employed, a similar dissociation between manual and saccadic responses would be observed for microsaccades.

This dissociation between the response modes did not occur for the exogenous condition when SI were affected equally by IOR. Interestingly, generation of IOR requires activation of oculomotor systems regardless of response mode (Ro et al., 2003) which is substantiated by the fact that IOR during manual endogenous conditions only occurs if a saccade to the cue has been prepared or executed (Rafal et al., 1989) and that IOR is influenced by a saccadic response being made to the cue or target (Taylor and Klein, 2000). This suggests that SI direction was not affected during the endogenous manual condition because oculomotor planning did not occur. Therefore, our findings indicate that under

conditions that demand an endogenous shift of attention without a subsequent saccade, minimal activation of the oculomotor system is required and that this may manifest as a decoupling of SI direction with attention orienting. This is in keeping with studies highlighting that task conditions may determine how closely attention and saccade planning are associated (Fischer, 1999; Abrams and Pratt, 2000; Taylor and Klein, 2000; Briand et al., 2000; Hunt and Kingstone, 2003; Sato and Schall, 2003; Ignashchenkova et al., 2004; Sumner et al., 2004; Thompson et al., 2005).

### 3.4. *Neural substrate of SI*

Previous research has suggested that the SC plays a key role in microsaccade production (Hafed and Clark, 2002; Rolfs et al., 2005; Laubrock et al., 2005) and as our work suggests a close link between microsaccades and SI, it is likely that SI also arise at the level of the SC. Evidence supporting SC involvement has been partly based on similarities between microsaccades and voluntary saccades such as their binocularity and adherence to the main sequence but evidence from the aforementioned microsaccade studies as well as the current results allows us to be more specific. Reaction times of larger voluntary saccades correlate strongly with target-related activity within the SC (Dorris and Munoz, 1998; Bell et al., 2004; Fecteau et al., 2004) so any resemblance between voluntary saccade and SI/microsaccade dynamics would suggest that microsaccades and SI may also be influenced by SC cell activity. Indeed, microsaccades, SI and voluntary saccades are all affected by the presence of IOR, a response which is considered to be in part generated at the level of the SC (Posner et al., 1985; Abrams and Dobkin, 1994; Sapir et al., 1999). Furthermore, all three saccade types exhibit similar post cue inhibition effects that have been attributed to increased SC rostral build up cell activity (Levy-Schoen, 1969; Walker et al., 1997; Reingold and Stampe, 2002, 2004). Moreover, SI displayed greater attenuation for exogenous neutral cues (illumination of both peripheral boxes) than exogenous directional cues (illumination of one peripheral box), a trend that was not observed for central endogenous cues. This is reminiscent of the remote distracter effect where two targets that are presented simultaneously in different hemifields delay reaction times (Levy-Schoen, 1969; Walker et al., 1997) and is thought to be due to increased SC rostral build up cell activity produced by the two targets.

The relationship between microsaccades and voluntary saccades has been examined more directly by Rolfs et al. (2005) who documented that microsaccade frequency decreased immediately before a voluntary saccade and if a microsaccade did occur before a saccade this caused a delay in saccade latency. This implies that both voluntary saccades and microsaccades rely on the same neural substrate, potentially the rostral SC build up cells. As discussed in the Introduction, rostral build up cells are active during small saccades in the amplitude range of microsaccades and SI, but conversely these cells must cease activity in order for a larger voluntary saccade to be produced (Gandhi and Keller, 1999; Munoz and Wurtz, 1992, 1993a,b, 1995a,b; Munoz and Istvan, 1998; Krauzlis et al., 2000). Rolfs and colleagues also observed a reaction time shortening effect for memory saccade trials if a micro-

saccade occurred towards the presented target and speculated that this was due to perceptual enhancement, motor enhancement or attention orientation. Our results linking SI to saccadic preparation would support the motor enhancement account, indicating that when microsaccades were directed towards the target on memory saccade trials, saccadic preparation was occurring.

In conclusion, SI characteristics are affected by changes in the level and orientation of exogenous and endogenous attention. The similarity with previously reported microsaccade characteristics suggests that SI and microsaccades are closely related and should perhaps be considered as the same type of fixation saccade. Although our observations are in keeping with a close link between eye movements and attention we also found that attention had less influence on SI under conditions where eye movements were not required, suggesting a degree of flexibility between the two systems. Finally, in line with previous work on microsaccades, the exploration of SI may also provide a useful tool in examining the relationship between eye movements and attention and that the use of attentional paradigms may assist in distinguishing those SI that are of a physiological origin from those that may represent pathology.

## 4. Experimental procedures

### 4.1. Subjects

We tested 12 healthy volunteers whose average age was 28.67 years (range, 19–42). The subjects had no previous or current history of ocular disease, strabismus, general health problems or medication that had been linked to any ocular complications. Subjects demonstrated a corrected visual acuity of 0.2

LogMAR or better in either eye. Each gave written informed consent to participate and the study was approved by a local ethical committee.

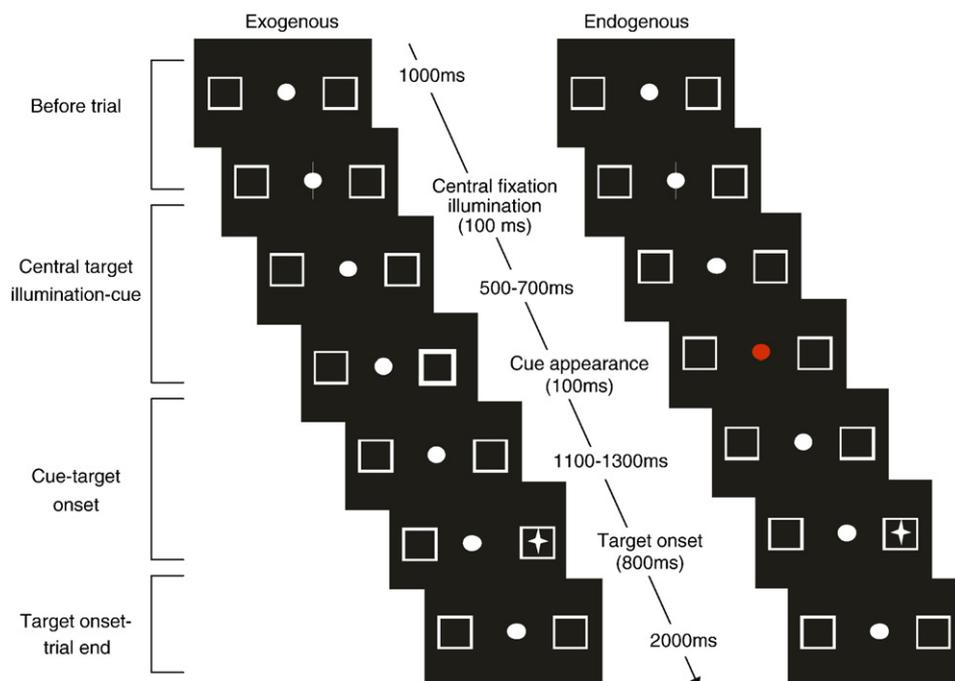
### 4.2. Eye movement recording and instrumentation

Horizontal eye movements were recorded binocularly using an IRIS 6500 infrared limbal tracker (Skalar Medical, Delft, The Netherlands). The analogue output was filtered through a 100-Hz low pass filter, digitised to 12-bit resolution and then sampled at intervals at 5 ms (200 Hz). The system was linear to  $\pm 20^\circ$  and had a resolution of  $>5'$ arc. Each subject's head was restrained using a chin rest and cheek pads.

Visual stimuli were displayed on a cathode ray tube computer monitor and viewed from a distance of 55 cm giving a field of  $27.1^\circ \times 38.5^\circ$ . They consisted of a central fixation circle ( $1.04^\circ$ ) that was flanked by two peripheral boxes ( $3.85^\circ \times 3.85^\circ$ ). The boxes were positioned  $13.02^\circ$  from the fixation circle. An asterisk ( $0.42^\circ$ ) served as the target and appeared in the centre of each box (Fig. 7). The distance between the central fixation target and the peripheral asterisk subtended  $14.58^\circ$ . Testing was carried out in a quiet, near dark room. Subject's eye movements were calibrated by moving a circular calibration target ( $0.42^\circ$ ) sinusoidally at 0.19 Hz over a horizontal range of  $\pm 17.7^\circ$ .

### 4.3. The experimental procedure

In order to gain baseline measurements of SI frequency, amplitude and directional bias (the percent of SI directed rightward) subjects were instructed to fixate a central point ( $0.42^\circ$ ) for 2 min. Following this they were required to perform two separate attention paradigms where the target was either cued exogenously or endogenously. Response mode to the



**Fig. 7** – Time course of exogenous (left figure) and endogenous (right figure) tasks. The different trial periods in which the SI were analysed are described to the left.

target could either be a manual button press or saccade giving a total of four separate tasks: (1) exogenous manual; (2) exogenous saccadic; (3) endogenous manual; and (4) endogenous saccadic. These tasks were performed separately and counterbalanced over two 75-min sessions.

#### 4.3.1. Exogenous task

Subjects were required to fixate the central circular point which was continually present throughout the trials. A trial began (Fig. 7a) with brightening (100 ms) of the central point. Following a pseudo-randomised delay of between 500 and 700 ms, the outline of one of the peripheral boxes would brighten for 100 ms. The subject was instructed to ignore this cue and continue fixating the central fixation point. There was then a further delay of 1100 or 1300 ms and the target (an asterisk) appeared randomly in one of the two peripheral boxes for 800 ms. Hence, non-predictive 50% valid cues were used to summon attention to the cue by pure exogenous mechanisms. Depending on response mode, the subject was required to either press a button (exogenous manual task) or make a saccade to the target, then back to the centre once it was extinguished (exogenous saccade task). A new trial commenced 3 s later with brightening of the central fixation point. Stimulus onset asynchrony (SOA), the time between the onset of the cue and the onset of the target was either 1200 or 1400 ms.

Eight conditions were tested: Cue location (left, right) × SOA (1200, 1400) × Target location (left, right). Each condition was repeated 12 times giving a total of 96 trials. Neutral trials, where the non-informative cue consisted of both peripheral boxes flashing, followed by the appearance of the target in one of the boxes occurred in 24 trials (20%) giving a grand total of 120 trials. The 120 trials were repeated under the two different response modes (manual and saccadic). The trials were separated into blocks of 40 and at the beginning of each, eye movements were calibrated.

#### 4.3.2. Endogenous condition

The timing of the trials was identical to the exogenous task (Fig. 7b). The difference was that the colour of a centrally presented cue informed the subject of the likely target location: Yellow=left, Blue=right, Red=non-informative neutral cue. The subject was instructed to use the information present in these cues but to continue fixating at the central fixation point. Hence central informative 80% valid cues (yellow/blue) were used to summon attention by pure endogenous mechanisms, in contrast to the non-informative (50% valid) red cue. Depending on the response mode, the subject was required to either press a button (endogenous manual task) or make a saccade to the target, then back to the centre once it was extinguished (endogenous saccade task). Circular colour cues (as opposed to arrow cues) were chosen so that any influence of cue form and shape on SI behaviour would be minimal and because arrow cues have been shown to involve an exogenous component.

Eight conditions were tested: Cue location (left, right) × SOA (1200, 1400) × Target location (left, right). The four conditions where the cue correctly predicted the target location were repeated 48 times and the four conditions where the cue incorrectly predicted the target were repeated 12 times giving a total of 240 trials. Neutral trials occurred in 60

trials (20%) giving a grand total of 300 trials. The 300 trials were conducted under the two different response modes. The trials were separated into blocks of 50 and at the beginning of each eye movements were calibrated.

### 4.4. Data analysis

#### 4.4.1. Saccadic and manual responses

Eye position was recorded binocularly to allow selection of conjugate saccades, but only data from the right eye were used in the analysis. Saccade start and end points were determined by a 20°/s cut-off criterion, using bespoke Matlab scripts, and the calculated amplitude and latency stored to disc. Artefacts such as blinks and drift were discarded together with data from trials where saccades were made in the direction opposite the target or where saccadic responses were <80 ms and >2 standard deviations from the average. Removal of such trials amounted to <12%. Trials with button responses <100 ms and >1000 ms were also removed (<1% of trials).

#### 4.4.2. SI analysis

SI start and end points were determined by a 20°/s cut-off criterion. SI with amplitudes >4° and durations >800 ms were not included in the analysis as it has been shown that these are the upper limits of SI (Abadi and Gowen, 2004). Once the SI were detected their initial direction (right or left) and amplitude were stored and were manually assigned to a category: Monophasic square wave intrusion, Biphasic square wave intrusion, Double saccadic pulse or Saccadic pulse (Abadi and Gowen, 2004). These all commence with an initial saccade but differ according to duration and whether the return movement consists of a saccade or drift. In order to conduct a more powerful analysis, all types were analysed together and collectively termed SI. A total of 24260 SI were collected.

Three SI parameters were calculated: SI amplitude, SI frequency (per minute) and the percent of SI directed towards the cue. For neutral trials, the percent of rightward directed SI was calculated instead of percent towards the cue. In order to record the effect of the different trial events on the SI, they were sorted according to:

- (1) Attention condition—whether they occurred during an exogenous or endogenous trial
- (2) Response mode—whether they occurred during a manual or saccadic trial
- (3) Trial period—what time they occurred. Trials were separated into four time periods: (a) before trial (1000 ms before the central cue illuminated); (b) central target illumination to cue onset; (c) cue to target onset (SOA); and (d) target onset to trial end (Fig. 7).
- (4) Cue type—whether they occurred in a trial where the cue appeared in the same/different direction as the target or where the cue was neutral.

As the interval between the cue and target was of particular interest we performed a separate analysis on this period by segregating it into bins of 12 × 100 ms bins and allocating the SI characteristic accordingly. For each subject and each time window, an average was computed and used in the statistical analysis.

#### 4.5. Statistical analysis

Data for SI amplitude (Shapiro–Wilk test,  $p=0.99$ ; mean = 0.62, median=0.63) and percent of SI directed towards the cue (Shapiro–Wilk test,  $p=0.81$ ; mean=0.46, median=0.46) were normally distributed whereas SI frequency was not; therefore non-parametric statistics were conducted on the latter. In cases where the data violated the assumption of sphericity, the Greenhouse–Geisser correction was employed.

#### Acknowledgments

We would like to thank Andrew Jerrison for his programming advice. This work was supported by James McDonnell Foundation and the Wellcome Trust.

#### REFERENCES

- Abadi, R.V., Gowen, E., 2004. Characteristics of saccadic intrusions. *Vision Res.* 44, 2675–2690.
- Abrams, R., Dobkin, R.S., 1994. The gap effect and inhibition of return: interactive effects on eye movement latencies. *Exp. Brain Res.* 98, 483–487.
- Abrams, R.A., Pratt, J., 2000. Oculocentric coding of inhibited eye movements to recently attended locations. *J. Exp. Psychol. Hum. Percept. Perform.* 26, 776–788.
- Awh, E., Armstrong, K.M., Moore, T., 2006. Visual and oculomotor selection: links, causes and implications for spatial attention. *Trends Cogn. Sci.* 10, 124–130.
- Barlow, H.B., 1952. Eye movements during fixation. *J. Physiol.* 116, 290–306.
- Bell, A.H., Fecteau, J.H., Munoz, D.P., 2004. Using auditory and visual stimuli to investigate the behavioral and neuronal consequences of reflexive covert orienting. *J. Neurophysiol.* 91, 2172–2184.
- Briand, K.A., Larrison, A.L., Sereno, A.B., 2000. Inhibition of return in manual and saccadic response systems. *Percept. Psychophys.* 62, 1512–1524.
- Carpenter, R.H.S., 1988. Chapter 6. Miniature eye movements. In: Carpenter, R.H.S. (Ed.), *Movements of the Eyes*. Pion Press, London, pp. 124–138.
- Corbetta, M., 1998. Frontoparietal cortical networks for directing attention and the eye to visual locations: identical, independent, or overlapping neural systems? *Proc. Natl. Acad. Sci. U. S. A.* 95, 831–838.
- Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev., Neurosci.* 3, 201–215.
- Deubel, H., 1995. Separate adaptive mechanisms for the control of reactive and volitional saccadic eye movements. *Vision Res.* 35, 3529–3540.
- Ditchburn, W., 1973. *Eye Movements and Visual Perception*. Clarendon Press, Oxford.
- Ditchburn, W., 1980. Letter to the editors. The function of small saccades. *Vision Res.* 20, 271–272.
- Ditchburn, W., Ginsborg, B.L., 1953. Involuntary eye movements during fixation. *J. Physiol.* 119, 1–17.
- Dorris, M.C., Munoz, D.P., 1998. Saccadic probability influences motor preparation signals and time to saccadic initiation. *J. Neurosci.* 18, 7015–7026.
- Engbert, R., 2006. Microsaccades: a microcosm for research on oculomotor control, attention, and visual perception. *Prog. Brain Res.* 154, 179–194.
- Engbert, R., Kliegl, R., 2003a. Microsaccades uncover the orientation of covert attention. *Vision Res.* 43, 1035–1045.
- Engbert, R., Kliegl, R., 2003b. Binocular coordination in microsaccades. In: Hyönä, J., Radach, R., Deubel, H. (Eds.), *The Mind's Eye: Cognitive and Applied Aspects of Eye Movements*. Amsterdam, Elsevier, pp. 103–117.
- Engbert, R., Mergenthaler, K., 2006. Microsaccades are triggered by low retinal image slip. *Proc. Natl. Acad. Sci. U. S. A.* 103, 7192–7197.
- Fecteau, J.H., Bell, A.H., Munoz, D.P., 2004. Neural correlates of the automatic and goal-driven biases in orienting spatial attention. *J. Neurophysiol.* 92, 1728–1737.
- Feldon, S.E., Langston, J.W., 1977. Square–Wave jerks: a disorder of microsaccades? *Neurology* 27, 278–281.
- Fischer, M.H., 1999. An investigation of attention allocation during sequential eye movement tasks. *Q. J. Exp. Psychol. A* 52, 649–677.
- Galfano, G., Betta, E., Turatto, M., 2004. Inhibition of return in microsaccades. *Exp. Brain Res.* 159, 400–404.
- Gandhi, N.J., Keller, E.L., 1999. Comparison of saccades perturbed by stimulation of the rostral superior colliculus, the caudal superior colliculus and the omnipause neuron region. *J. Neurophysiol.* 82, 3236–3253.
- Gibson, B.S., Bryant, T.A., 2005. Variation in cue duration reveals top-down modulation of involuntary orienting to uninformative symbolic cues. *Percept. Psychophys.* 67, 749–758.
- Gowen, E., Abadi, R.V., 2005. Saccadic instabilities and voluntary saccade behaviour. *Exp. Brain Res.* 164, 29–40.
- Gowen, E., Abadi, R.V., Poliakoff, E., 2005. Paying attention to saccadic intrusions. *Cogn. Brain Res.* 25 (3), 810–825.
- Grosbras, M.H., Laird, A.R., Paus, T., 2005. Cortical regions involved in eye movements, shifts of attention, and gaze perception. *Hum. Brain Mapp.* 25, 140–154.
- Hafed, Z.M., Clark, J.J., 2002. Microsaccades as an overt measure of covert attention shifts. *Vision Res.* 42, 2533–2545.
- Herishanu, Y.O., Sharpe, J.A., 1981. Normal square wave jerks. *Investig. Ophthalmol. Vision Sci.* 20, 268–272.
- Hunt, A.R., Kingstone, A., 2003. Inhibition of return: dissociating attentional and oculomotor components. *J. Exp. Psychol. Hum. Percept. Perform.* 29, 1068–1074.
- Ignashchenkova, A., Dicke, P.W., Haarmeier, T., Thier, P., 2004. Neuron-specific contribution of the superior colliculus to overt and covert shifts of attention. *Nat. Neurosci.* 7, 56–64.
- Klein, R.M., 1980. Does oculomotor readiness mediate cognitive control of visual attention? In: Nickerson, R. (Ed.), *Attention and Performance*, vol. VIII. Erlbaum, Hillsdale, NJ.
- Klein, R.M., 2000. Inhibition of return. *Trends Cogn. Sci.* 4, 138–147.
- Klein, R.M., Shore, D.I., 2000. Chapter 8. Relations among modes of visual orienting. In: Monsell, S., Driver, J. (Eds.), *Control of Cognitive Processes. Attention and Performance XV111*. The MIT Press, Cambridge, MA, pp. 195–208.
- Kowler, E., 1991. The stability of gaze and its implications for vision. In: Carpenter, R.H.S. (Ed.), *Vision and Visual Dysfunction. Eye Movements*, vol. 8, pp. 71–92.
- Kowler, E., Steinman, R.M., 1980. Small Saccades serve no useful purpose: reply to a letter by R.W. Ditchburn. *Vision Res.* 20, 273–276.
- Kowler, E., Anderson, E., Doshier, B., Blaser, E., 1995. The role of attention in the programming of saccades. *Vision Res.* 35, 1897–1916.
- Krauzlis, R.J., Basso, M.A., Wurtz, R.H., 2000. Discharge properties of neurons in the rostral superior colliculus of the monkey during smooth-pursuit eye movements. *J. Neurophysiol.* 84, 876–891.
- Laubrock, J., Engbert, R., Kliegl, R., 2005. Microsaccade dynamics during covert attention. *Vision Res.* 45, 721–730.
- Levy-Schoen, A., 1969. Determination et latence de la réponse oculomotrice a deux stimulus. *L'Anne Psychol.* 74, 43–66.

- Martinez-Conde, S., Macknik, S.L., Hubel, D.H., 2004. The role of fixational eye movements in visual perception. *Nat. Rev., Neurosci.* 5, 229–240.
- Mayer, A.R., Dorflinger, J.M., Rao, S.M., Seidenberg, M., 2004. Neural networks underlying endogenous and exogenous visual-spatial orienting. *NeuroImage* 23, 534–541.
- Moller, F., Laursen, M.L., Tygesen, J., Sjolie, A.K., 2002. Binocular quantification and characterization of microsaccades. *Graefes Arch. Clin. Exp. Ophthalmol.* 240, 765–770.
- Mort, D.J., Perry, R.J., Mannan, S.K., Hodgson, T.L., Anderson, E., Quest, R., McRobbie, D., McBride, A., Husain, M., Kennard, C., 2003. Differential cortical activation during voluntary and reflexive saccades in man. *NeuroImage* 18, 231–246.
- Muller, H.J., Rabbitt, P.M., 1989. Reflexive and voluntary orienting of visual attention: time course of activation and resistance to interruption. *J. Exp. Psychol. Hum. Percept. Perform.* 15, 315–330.
- Munoz, D.P., Istvan, P.J., 1998. Lateral inhibitory interactions in the intermediate layers of the monkey superior colliculus. *J. Neurophysiol.* 79, 1193–1209.
- Munoz, D.P., Wurtz, R.H., 1992. Role of the rostral superior colliculus in active visual fixation and execution of express saccades. *J. Neurophysiol.* 67, 1000–1002.
- Munoz, D.P., Wurtz, R.H., 1993a. Fixation cells in monkey superior colliculus: 1. Characteristics of cell discharge. *J. Neurophysiol.* 70, 559–575.
- Munoz, D.P., Wurtz, R.H., 1993b. Fixation cells in monkey superior colliculus: II. Reversible activation and deactivation. *J. Neurophysiol.* 70, 576–589.
- Munoz, D.P., Wurtz, R.H., 1995a. Saccade-related activity in monkey superior colliculus: I. Characteristics of burst and buildup cells. *J. Neurophysiol.* 73, 2313–2333.
- Munoz, D.P., Wurtz, R.H., 1995b. Saccade-related activity in monkey superior colliculus: II. Spread of activity during saccades. *J. Neurophysiol.* 73, 2334–2348.
- Nobre, A.C., Gitelman, D.R., Dias, E.C., Mesulam, M.M., 2000. Covert visual spatial orienting and saccades: overlapping neural systems. *NeuroImage* 11, 210–216.
- Ohtsuka, K., Mukono, K., Ukai, K., Ishikawa, S., 1986. The origin of square wave jerks: conditions of fixation and microsaccades. *Jpn. J. Ophthalmol.* 30, 209–215.
- Peelen, M.V., Heslenfeld, D.J., Theeuwes, J., 2004. Endogenous and exogenous attention shifts are mediated by the same large-scale neural network. *NeuroImage* 22, 822–830.
- Posner, M.I., 1980. Orienting of attention. *Q. J. Exp. Psychol.* 32, 3–25.
- Posner, M.I., Cohen, Y., 1984. Components of visual orienting. In: Bouma, H., Bouwhuis, D. (Eds.), *Attention and Performance*, pp. 531–556. London.
- Posner, M.I., Snyder, C.R.R., Davidson, B.J., 1980. Attention and the detection of signals. *J. Exp. Psychol.* 109, 160–174.
- Posner, M.I., Rafal, R., Choate, L.S., Vaughan, J., 1985. Inhibition of return: neural basis and function. *Cogn. Neuropsychol.* 2, 211–228.
- Rafal, R., Henik, A., 1994. The neurology of inhibition integrating controlled and automatic processes. In: Dagenbach, D., Carr, T.H. (Eds.), *Inhibitory Processes in Attention, Memory and Language*. Academic Press, San Diego, pp. 1–51.
- Rafal, R., Calabresi, P.A., Brennan, C.W., Sciolto, T.K., 1989. Saccade preparation inhibits reorienting to recently attended locations. *J. Exp. Psychol. Hum. Percept. Perform.* 15 (4), 673–685.
- Ratliff, F., Riggs, L.A., 1950. Involuntary motions of the eye during monocular fixation. *J. Exp. Psychol.* 40, 687–701.
- Reingold, E.M., Stampe, D.M., 2002. Saccadic inhibition in voluntary and reflexive saccades. *J. Cogn. Neurosci.* 14, 371–388.
- Reingold, E.M., Stampe, D.M., 2004. Saccadic inhibition in reading. *J. Exp. Psychol. Hum. Percept. Perform.* 30, 194–211.
- Rizzolatti, G., Riggio, L., Drascola, I., Umilta, C., 1987. Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. *Neuropsychologia* 25, 31–40.
- Ro, T., Farne, A., Chang, E., 2003. Inhibition of return and the human frontal eye fields. *Exp. Brain Res.* 150, 290–296.
- Rolfs, M., Engbert, R., Kliegl, R., 2004. Microsaccade orientation supports attentional enhancement opposite a peripheral cue: commentary on Tse, Sheinberg, and Logothetis 2003. *Psychol. Sci.* 15, 705–707.
- Rolfs, M., Laubrock, J., Kliegl, R., 2005. Shortening and prolongation of saccade latencies following microsaccades. *Exp. Brain Res.* 169, 369–376.
- Sapir, A., Soroker, N., Berger, A., Henik, A., 1999. Inhibition of return in spatial attention: direct evidence for collicular generation. *Nat. Neurosci.* 2, 1053–1054.
- Sato, T.R., Schall, J.D., 2003. Effects of stimulus-response compatibility on neural selection in frontal eye field. *Neuron* 38, 637–648.
- Shallo-Hoffmann, J., Petersen, J., Muhlendyck, H., 1989. How normal are “normal” square wave jerks. *Investigative Ophthalmology and Vision Science* 30, 1009–1011.
- Shallo-Hoffmann, J., Sendler, B., Muhlendyck, H., 1990. Normal square wave jerks in differing age groups. *Investig. Ophthalmol. Vision Sci.* 31, 1649–1652.
- Shepherd, M., Findlay, J.M., Hockey, R., 1986. The relationship between eye movements and spatial attention. *Q. J. Exp. Psychol. A* 38, 475–491.
- Simon, J.R., 1990. The effects of an irrelevant directional cue on human information processing. In: Proctor, R.W., Reeve, T.G. (Eds.), *Stimulus Response Compatibility: An integrated Perspective*. Adv. Psychol., vol. 65. North Holland, Amsterdam, pp. 31–86.
- Steinman, R.M., 1965. Effect of target size, luminance and color on monocular fixation. *J. Opt. Soc. Am.* 55, 1158–1165.
- Steinman, R.M., Cunitz, R.J., Timberlake, G.T., Herman, M., 1967. Voluntary control of microsaccades during maintained monocular fixation. *Science* 155, 1577–1579.
- Steinman, R.M., Haddad, G.M., Skavenski, A.A., Wyman, D., 1973. Miniature eye movements. *Science* 181, 810–819.
- Steinman, R.M., Cushman, W.B., Martins, A.J., 1982. The precision of gaze. *Hum. Neurobiol.* 1, 97–109.
- Sumner, P., Nachev, P., Vora, N., Husain, M., Kennard, C., 2004. Distinct cortical and collicular mechanisms of inhibition of return revealed with s cone stimuli. *Curr. Biol.* 14, 2259–2263.
- Tassinari, G., Aglioti, L., Chelazzi, L., Marzi, C.A., Belucchi, G., 1987. Distribution in the visual field of the costs of voluntarily allocated attention and of the inhibitory after-effects of covert orienting. *Neuropsychologia* 25, 55–71.
- Taylor, T.L., Klein, R.M., 2000. Visual and motor effects in inhibition of return. *J. Exp. Psychol. Hum. Percept. Perform.* 26, 1639–1656.
- Theeuwes, J., Kramer, A.F., Hahn, S., Irwin, D.E., 1998. Our eyes do not always go where we want them to go: capture of the eyes by new objects. *Psychol. Science* 9, 379–385.
- Thompson, K.G., Biscoe, K.L., Sato, T.R., 2005. Neuronal basis of covert spatial attention in the frontal eye field. *J. Neurosci.* 25, 9479–9487.
- Tse, P.U., Sheinberg, D.L., Logothetis, N.K., 2002. Fixational eye movements are not affected by abrupt onsets that capture attention. *Vision Res.* 42, 1663–1669.
- Walker, R., Deubel, H., Schneider, W.X., Findlay, J.M., 1997. Effect of remote distractors on saccade programming: evidence for an extended fixation zone. *J. Neurophysiol.* 78, 1108–1119.
- Westheimer, G., McKee, S.P., 1975. Visual acuity in the presence of retinal image motion. *J. Opt. Soc. Am.* 65, 847–850.
- Winterson, B.J., Collewijn, H., 1976. Microsaccades during finely guided visuomotor tasks. *Vision Res.* 16, 1387–1390.