RESEARCH ARTICLE

Evidence for an attentional component in saccadic inhibition of return

David Souto · Dirk Kerzel

Abstract After presentation of a peripheral cue, facilitation at the cued location is followed by inhibition of return (IOR). It has been recently proposed that IOR may originate at different processing stages for manual and ocular responses, with manual IOR resulting from inhibited attentional orienting, and ocular IOR resulting form inhibited motor preparation. Contrary to this interpretation, we found an effect of target contrast on saccadic IOR. The effect of contrast decreased with increasing reaction times (RTs) for saccades, but not for manual key-press responses. This may have masked the effect of contrast on IOR with saccades in previous studies (Hunt and Kingstone in J Exp Psychol Hum Percept Perform 29:1068–1074, 2003) because only mean RTs were considered. We also found that background luminance strongly influenced the effects of gap and target contrast on IOR.

Keywords IOR · Saccades · Attention · Motor preparation · Background luminance

Introduction

Inhibition of return (IOR) is the slowing of responses to targets appearing at a previously cued peripheral location. It occurs from 300 ms to several seconds after cue onset. Several alternative explanations of this effect have been proposed. They can be roughly parsed into attentional/

D. Souto (✉) · D. Kerzel
Faculté de Psychologie et Sciences de l'Éducation,
Université de Genève, 40 bd du Pont d'Arve,
1205 Geneva, Switzerland
e-mail: david.souto@unige.ch

perceptual and motor explanations (e.g. Posner and Cohen 1984). Among the possible mechanisms, the attentional momentum hypothesis states that attention overshoots the fixation point when it returns from the peripheral cue. As a result, there is attentional enhancement opposite to the cued location (e.g. Spalek and Hammad 2004; but see Machado and Rafal 2004). However, IOR cannot be unequivocally accounted for by an attention shift. For instance, it is difficult to find IOR with discrimination tasks (for a graphical meta-analysis see Fig. 1 in Ivanoff and Klein 2006), and with perceptual measures of attention such as temporal order judgments (Maylor 1985; but see Gibson and Egeth 1994) or illusory line motion (Schmidt 1996). IOR must therefore be more than the direct consequence of prior facilitation. It has also been shown to be more than the carry-over of an inhibitory set induced by the instruction to ignore the cue, as IOR is found even in target–target paradigms (Welsh and Pratt 2006). In contrast, the mere programming of a saccade (without a cue capturing attention) is enough to produce IOR (Rafal et al. 1989), which is the main behavioral evidence supporting the role of eye movement programming in the generation of IOR.

The motor bias account states that IOR arises from voluntary or reflexive programming of eye movements. Activation of a motor program, regardless of whether it is executed or cancelled, slows down subsequent motor actions directed towards the cued location (Taylor and Klein 1998, 2000). Accordingly, IOR is found with central as well as peripheral cues (Rafal et al. 1989; Taylor and Klein 2000). Additional support for a privileged role of the oculomotor system in the generation of IOR comes from the involvement of the superior colliculus in IOR (Sapir et al. 1999; but see Smith et al. 2004) and from the fact that IOR is stronger with saccades than with manual pointing responses (Fischer et al. 2003; Pratt and Neggers 2008).
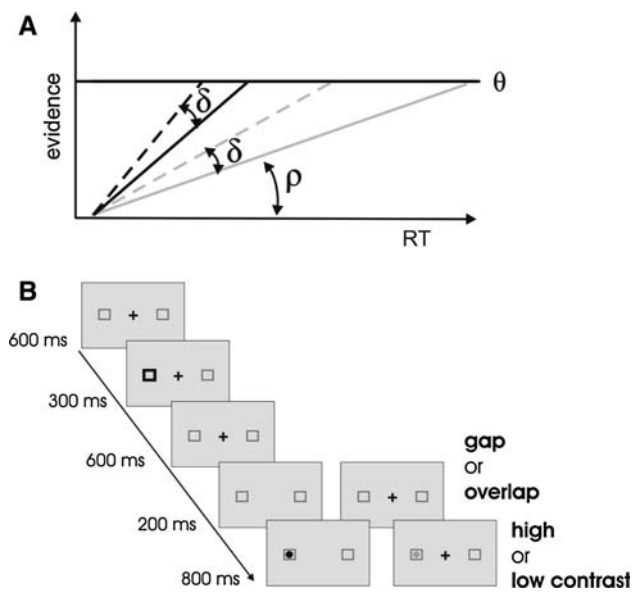
Fig. 1 Experimental predictions and paradigm. **a** explains why the contrast manipulation is an indicator for the involvement of attention (see Reuter-Lorenz et al. 1991; Hawkins et al. 1988). This conceptualization is based upon a rise-to-threshold model of reaction times (akin to the LATER model, e.g. Carpenter and Williams 1995). *Diagonal lines* represent the accrual of information ("evidence") after target onset. Once evidence has reached some threshold level θ, the decision to move is made. This model can explain the way target contrast affects attentional benefits. The *gray line* with slope ρ represents the accrual of evidence for a low contrast target in the absence of any cue (baseline condition, *solid gray line*), and δ represents the increase of this rate due to attention (attention condition, *dotted gray line*). *Black lines* represent the accrual of evidence with high-contrast targets. The threshold is reached faster in the baseline condition with high-contrast targets because of faster accrual with high- than with low-contrast targets (compare *solid gray* and *solid black* lines). Despite an identical increase of the accrual rate δ, attention has a larger effect on reaction times with low-contrast targets than with high-contrast targets (compare the difference between *solid* and *dotted lines* for *black* and *gray lines*). Thus additive effects on slopes result in multiplicative effects on latencies. **b** shows stimuli and time-course in Experiment 1. The fixation cross either disappeared 200 ms before target onset (gap) or remained visible throughout (overlap). The target was either *black* (high contrast) or *gray* (low contrast). A valid trial is depicted in which the target appears at the cued location 1.1 s after cue onset

Further, some studies have employed the gap effect (i.e., the shortening of saccadic latencies when the fixation stimulus is removed some time before target onset) to test whether IOR affects the motor preparation stage. It is known that the gap effect has a motor component, and is independent of attentional facilitation (e.g. Reuter-Lorenz et al. 1991). Following Sternberg's additive factors logic (Sternberg 1969), interactive effects should be expected if both effects share a common stage. Indeed, IOR was found to interact with the gap effect (Abrams and Dobkin 1994). However, there is no consensus on the nature of the interaction. Different studies reported contradictory results (Abrams and Dobkin 1994; Hunt and Kingstone 2003).

On the other hand, many studies found evidence that attention contributes to IOR, indicating that it is the consequence of both motor and attentional biases (Kingstone and Pratt 1999; Taylor and Klein 2000; Sumner et al. 2004). For instance, reliable IOR was found in conditions that should not elicit a motor bias. When a symbolic and uninformative cue was presented and the response was a choice key-press to a peripheral target, IOR was observed (Taylor and Klein 2000), possibly because of the automatic attentional orienting by arrow cues (Tipples 2002). Another argument for an attentional component in IOR is provided by an effect of target luminance[1] on IOR (Reuter-Lorenz et al. 1996; Hunt and Kingstone 2003). Because effects of attention on visual detection are larger with weak compared to strong signals (Hawkins et al. 1988), IOR should be stronger with low-contrast targets than with high-contrast targets, presumably because of a lack of attention on the cued side. A possible mechanism for effects of target contrast on IOR is depicted in Fig. 1a. If the effect of attention was to increase the rate of accrual of evidence, benefits of attention on latency should be greater when the rate of accrual is low, as with low-contrast targets (Hawkins et al. 1988). Consistent with an attentional component, IOR was found to be larger with dim (low-contrast) than with bright (high-contrast) targets (Reuter-Lorenz et al. 1996; Hunt and Kingstone 2003).

Further, the gap effect (on saccadic RT) is additive with the effect of luminance (Reuter-Lorenz et al. 1991; Kingstone and Klein 1993a, b), suggesting that it does not result from attentional facilitation. Exploiting this property, Hunt and Kingstone (2003) examined effects of gap and target contrast on IOR with saccadic and key-press responses. IOR was affected by the gap effect only when measured with saccadic responses, suggesting that the motor component of IOR affects movements specifically directed at the cued location. Because key-presses were executed on a keyboard and never directed at the cued location, the effect of gap on IOR was absent for key-presses. Importantly, IOR was affected by target contrast only with key-press responses, but not with saccades, suggesting that IOR in saccadic responses had no effect on the perceptual stage. This finding is surprising in light of the close relation between attention and saccade programming. It is well known that attention is needed at the target location for the generation of voluntary saccades (Deubel and Schneider 1996). Attention to non-target locations can curve saccadic trajectories (Sheliga et al. 1994, 1995), or delay saccadic latency (e.g. Shepherd et al. 1986). Also, ample physiological evidence confirms the involvement of premotor structures in both attention

---

[1] To avoid ambiguities, we mostly refer to target luminance relative to background luminance (i.e., target contrast) instead of absolute luminance.

shifts and eye movements (e.g. Ignashchenkova et al. 2004). Temporally disrupting neuronal activity in one such interface between attention and eye movements, the frontal eye field (FEF), eliminated IOR with manual responses (Ro et al. 2003).

Our main concern was to reexamine the presence of perceptual and motor components in IOR with saccadic and key-press responses. We specifically looked at the effects of gap and target contrast on IOR, and the evolution of these effects across reaction time bins. To anticipate the results, the effect of luminance on IOR confirms an attentional component with saccadic responses, which is in line with a premotor conception of covert attention. Our results show also a dependence of IOR on background luminance, an unexpected finding that may support differential contributions of the parvo- and magnocellular system in the generation of IOR.

Experiment 1: perceptual and motor components with saccadic and key-press responses

Method

Subjects

There were 22 participants in this study ($M = 22$ years, $SD = 4$ years). Eighteen students participated in partial fulfillment of class requirements. Four were experienced observers in psychophysical studies and all were naïve with respect to the purpose of the experiment. Experiments were done in compliance with the Helsinki Declaration of 1964 and the ethical regulations of the University of Geneva.

Materials and stimuli

Head movements were constrained by a chinrest at a distance of 46 cm from a 100 Hz CRT monitor. Eye movements were monitored with a head-mounted eyetracker (Eyelink II, Ontario, Osgoode) set in pupil centroid mode, with a sampling frequency of 250 Hz. Calibration was achieved by fixation of three locations presented along a horizontal line. Only the horizontal eye position was sampled. The mean spatial error when retesting the same locations was less than half a degree.

Stimuli and trial time-course are depicted in Fig. 1b. In the first screen, two square placeholders ($0.9 \times 0.9°$, 23.3 cd/m^2) were presented at 6° (center-to-center) from a fixation cross ($0.2 \times 0.2°$, 0 cd/m^2) for 600 ms. The cue was a thickening (from 0.04° to 0.3°) and dimming (from 23.3 cd/m^2 to 0 cd/m^2) of the box outline and was presented for 300 ms. After 600 ms, the fixation cross was removed for 200 ms in the *gap* condition, whereas it remained on the

screen in the *overlap* condition. After this period the target was presented inside one of the two placeholders for 800 ms. The target ($0.4° \times 0.4°$) was of *low-contrast* (27.4 cd/m^2, Weber contrast of 7.1%) or *high-contrast* (0 cd/m^2, Weber contrast of 100%). The background luminance was light gray, 29.5 cd/m^2. Weber contrast is the difference between the stimulus and the background luminance divided by the background luminance. The contrast of the dim and bright targets in Hunt and Kingstone (2003) were 55 and 1453%, respectively. Their luminance values were 6.7, 10.4, and 104.1 cd/m^2 for background, dim, and bright targets, respectively. The decrease of reaction times with increasing stimulus contrast is much steeper for contrasts below 10% than it is for larger contrasts (e.g. Murray and Plainis 2003). Therefore, we expect larger benefits of attention in our experiment, because we used a contrast of 7.1% for our low-contrast target.

Procedure

The two response modes were tested in two sessions on different days. The order of sessions was balanced across subjects. Gap, target contrast, cue side (left or right), and cue validity were randomized within a block. There were 40 repetitions for each combination of response mode, gap, target contrast, and validity, amounting to at least 320 trials per session. Error trials were repeated at a random position in the remainder of the block. Participants were instructed to foveate the target or to press a left or right key of a game pad as fast as they could without making anticipation errors. They were told that the cue did not predict the location of the target, and therefore should be ignored. Participants triggered the next trial by pressing the two lateral keys of the game pad simultaneously. Saccades had to be larger than 1° and to occur no sooner than 50 ms after target onset, and no later than 600 ms (that is, more than 3 SD above median latency). Manual responses had to occur within 100–700 ms after target onset ($>M + 3$ SD). A low percentage of saccadic responses was anticipatory (5%), timed-out (0.5%) or in the wrong direction (1%); for manual responses, these proportions were 0.3, 1.2 and 1.3%, respectively.

Results

We calculated median response times for each subject and combination of response mode, gap, target contrast, and validity. Absolute latencies and IOR (valid minus invalid) are shown in Table 1 and Fig. 2, respectively. Inspection of Fig. 2a shows that the most prominent effects are stronger IOR with saccadic compared to manual responses, and stronger IOR with low- compared to high-contrast targets. A four-way, repeated-measures ANOVA (response

Table 1 Mean reaction time (RT) and between-subject standard error of the mean in Experiments 1 and 2 in the format $M \pm SE$. Inhibition of return (IOR) is the difference between invalid and valid conditions

| | Experiment 1 (N = 22) | | | | | |
| | Saccadic RT (ms) | | | Manual RT (ms) | | |
	Invalid	Valid	IOR	Invalid	Valid	IOR
Gap						
High contrast	178 ± 6	155 ± 6	23	319 ± 9	298 ± 8	21
Low contrast	228 ± 10	187 ± 7	41	365 ± 10	336 ± 9	29
Overlap						
High contrast	231 ± 8	207 ± 6	24	325 ± 10	312 ± 8	13
Low contrast	274 ± 9	241 ± 8	33	372 ± 10	349 ± 9	23
	Experiment 2 (N = 18, saccadic responses)					
	Light background			Dark background		
	Invalid	Valid	IOR	Invalid	Valid	IOR
Step						
High contrast	212 ± 9	189 ± 8	23	203 ± 8	181 ± 5	22
Low contrast	258 ± 10	211 ± 8	47	211 ± 8	192 ± 6	19
Overlap						
High contrast	246 ± 12	204 ± 8	42	237 ± 12	206 ± 9	31
Low contrast	305 ± 15	262 ± 11	43	276 ± 14	219 ± 9	57

mode × gap × target contrast × validity) was run on median RTs. Note that IOR should result in faster RTs in invalid than valid trials. Unsurprisingly, saccadic responses were 120 ms faster than manual responses (212 versus 334 ms), $F(1,21) = 149.7$, $p < 0.001$. A 30 ms gap effect was found, $F(1,21) = 90.7$, $p < 0.001$, that was greater with saccadic than manual reaction times (51 vs. 9 ms), $F(1, 21) = 53.6$, $p < 0.001$. IOR was of 26 ms, $F(1,21) = 87.7$, $p < 0.001$, and was also modulated by responses mode, $F(1,21) = 4.76$, $p < 0.05$, indicating slightly stronger IOR with saccadic than with key-press responses (29 vs. 22 ms).

There was no significant interaction between gap and validity, $F < 2.15$, $p = 0.16$. Further, latencies were about 40 ms longer for low-contrast compared to high-contrast targets, $F(1, 21) = 148.5$, $p < 0.001$, irrespective of response mode, $F < 1$. The effect of target contrast is numerically larger than in Hunt and Kingstone's (2003) study. They reported a difference of 17 ms between dim and bright targets (calculated from their Table 1). Thus, our study accentuates effects of target contrast which may have increased our chances of finding interactions involving target contrast.

Importantly, the effect of validity was modulated by target contrast, $F(1,21) = 17.1$, $p < 0.001$, indicating greater IOR with low- compared to high-contrast targets (32 vs. 20 ms). This interaction was not modulated by response mode, $F < 1$.

Hunt and Kingstone's (2003) most surprising result was the absence of a validity by target contrast interaction for saccadic responses. We ran separate ANOVAs (gap × target contrast × validity) for each response mode to follow-up on their results. The interaction between validity and target contrast was confirmed for saccades,

Fig. 2 Mean inhibition of return (*IOR* invalid RT minus valid RT) as a function of response mode, gap, and target contrast (*low C* low contrast, *high C* high contrast) is shown in **a**. **b** shows IOR as a function of quintile. For each quartile, IOR is computed and plotted against mean latency of invalid and valid RT. **c** shows ex-Gaussian fits to the quartiles underlying **b**, but only saccadic responses are shown. *Error-bars* represent the between-subject standard error of the mean
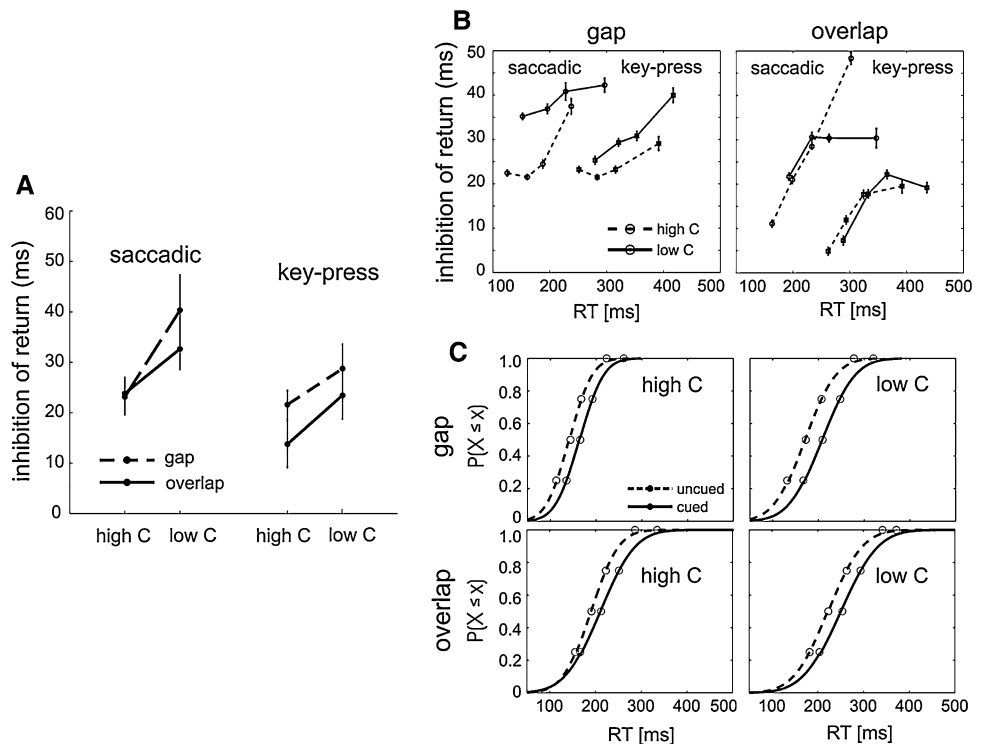
$F(1,21) = 18.5$, $p < 0.001$, and manual responses, $F(1,21) = 4.61$, $p < 0.05$. IOR increased by 15 ms with low-contrast compared to high-contrast targets for saccades (37 vs. 23 ms) and by 7 ms for manual responses (25 vs. 18 ms). We also confirmed a significant gap effect for manual (9 ms), $F(1,21) = 27.4$, $p < 0.001$, and saccadic responses (51 ms), $F(1,21) = 79.4$, $p < 0.001$. A small but significant gap effect with manual responses is not without precedent (Bekkering et al. 1996).

IOR as a function of responses time quantile

The discrepancy between Hunt and Kingstone's (2003) and our results may arise from two methodological differences. First, Hunt and Kingstone used means as a measure of the central tendency and we used medians. While means are frequently used, they will be strongly biased by long RTs when the distributions are skewed. Second, Hunt and Kingstone did not report any form of data trimming such that outlying data points may have contaminated the results.

To look for effects of IOR as a function of RT (see Ratcliff 1979), RTs were rank ordered separately for each participant and condition. Then, the observations were divided into four quartiles, so that each quartile contained 25% of the observations. IOR for each quartile is shown as a function of average quartile latency in Fig. 2b. The pattern in Fig. 2b may explain why the interaction between IOR and target contrast was missed when means were calculated. The difference between low- and high-contrast targets diminished with longer saccadic reaction times, and was even inverted in the overlap condition, as indicated by nearly 20 ms greater IOR with high-contrast targets in the last quartile (*t* test, $p = 0.06$). In the gap condition, only the first three quartiles showed significantly larger saccadic IOR with low compared to high contrast ($p < 0.02$). In the overlap condition, this was only the case in the first quartile ($p < 0.05$). The tendency for effects of target contrast on IOR to diminish with longer reaction times is nearly absent with key-press responses (i.e., the shape of the distribution for high- and low-contrast targets is very similar), and thus the effect of target contrast on IOR may be harder to obfuscate by averaging. This might explain why Hunt and Kingstone (2003) found an effect of luminance on IOR with manual responses, but not with saccades.

This relation is further illustrated in Fig. 2c, by showing the ex-Gaussian[2] fits to the latency quartiles in valid and invalid trials for saccadic responses (IOR values in Fig. 2b

---

[2] The SIMPLEX algorithm (MATLAB® function *fminsearch*, with default parameters) was used to find the best fitting ex-Gaussian cumulative distribution that minimized the squared sum of the residuals. The ex-Gaussian distribution is widely used as it usually offers a good fit of reaction times data (Heathcote et al. 1991; Luce 1991).

can be derived from the data points in Fig. 2c). Shorter RTs are visible in a shift of the distribution to the left. It is evident that RT distributions in valid trials are shifted to the left compared to invalid trials (compare solid and broken lines). The lower left panel in Fig. 2c shows the RT distributions underlying the sharp increase in IOR seen in the overlap condition with saccadic RTs and high-contrast targets (cf. Fig. 2b, right panel). Put another way, the left shift for cued targets is not uniform across the RT distribution, but increases with increasing RT.

Experiment 2: effect of background luminance with saccadic responses

As we found effects contrary to those reported by Hunt and Kingstone (2003) with saccadic responses, we replicated their display more closely. First, background luminance in their study was much darker than in our Experiment 1. Therefore, we added a condition with reduced background luminance. Second, we used a 0-ms gap/overlap paradigm as they did, instead of the 200-ms gap/overlap paradigm used in Experiment 1. In a previous study, the 200-ms gap led to somewhat larger IOR and shorter latencies than the 0-ms gap (Abrams and Dobkin 1994).

Method

Subjects

There were 18 observers (M = 24 years, SD = 5 years), 17 students naïve to the purpose of the experiment, and one experienced observer who already participated in the first experiment.

Stimuli and procedure

Methods were the same as in the first experiment, except for the following. Instead of a 200-ms gap, a 0-ms gap was used, which will be referred to as "step". We added two background luminance conditions as a blocked variable. Only saccadic responses were tested. Background luminance was light gray (29.5 cd/m^2) as in our first experiment, or dark (6.8 cd/m^2), which is about the same as in Hunt and Kingstone's (2003) study (6.7 cd/m^2). The targets in the light background condition were the same as in Experiment 1. The dim and bright targets in the dark background condition had a luminance of 10.3 and 58.8 cd/m^2, resulting in Weber contrasts of 51 and 764%, respectively. The low-contrast target had a higher contrast in the dark background condition than in the light background condition (51 vs. 7.1% Weber contrast), but matched the contrast value of 55% in Hunt and Kingstone

(2003). In the dark background condition, the placeholders, cue, and fixation target were white (58.8 cd/m^2). In both background luminance conditions, the cue was a thickening of the placeholder outline, not a dimming *and* thickening as in Experiment 1. With the exception of background luminance, all experimental factors (gap, target contrast, cue side, and cue validity) were randomized within a block. These differences are sketched in the insets of Fig. 3. There were 20 trials per condition (2 background luminance × 2 gap × 2 target contrast × 2 validity). The RT distribution (i.e., quartiles) was not analyzed because of the lower number of trials per condition.

Results

Results of the second experiment are summarized in Fig. 3. Absolute latencies are shown in Table 1. As in the first experiment, a large effect of target contrast on IOR was confirmed for light and dark background conditions. However, there was an interaction between validity, gap, and background luminance that complicates the picture. With the light background, the effect of target contrast on IOR was much larger in the step than in the overlap condition. A similar tendency can be seen in Experiment 1, where the effect of contrast was larger in the gap than in the overlap condition. With a dark background, the difference between step and overlap was reversed. The effect of target contrast on IOR was much larger in the overlap than in the step condition. This triple interaction can also be described as an interaction of gap and validity that is specific to dark targets: Inspection of Fig. 3 shows that the difference between
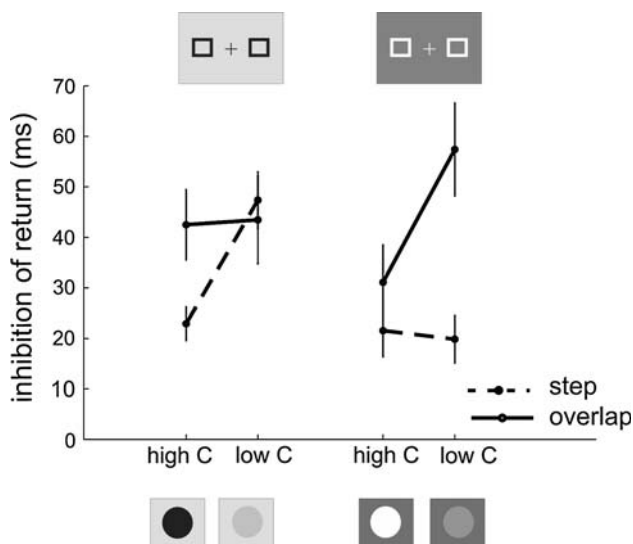

Fig. 3 Mean inhibition of return (invalid RT minus valid RT) as a function of target contrast, gap and background luminance. *Error-bars* represent the between-subject standard error of the mean

step and overlap is largest for dark targets (leftmost and rightmost data points).

A four-way repeated measures ANOVA (background × gap × target contrast × validity) was run on median saccadic latencies. There was a gap effect of 37 ms (244 vs. 207 ms), $F(1,17) = 68.14$, $p < 0.001$, and an effect of target contrast of 32 ms (242 vs. 210 ms), $F(1,17) = 137.5$, $p < 0.001$. Gap and target contrast interacted, $F(1,17) = 16.93$, $p < 0.001$, indicating that the gap effect was larger with low-contrast targets than with high-contrast targets (48 vs. 27 ms). Following the logic illustrated in Fig. 1a, the interaction with target contrast suggests that attention is involved in the gap effect. In contrast, no interaction of gap and target contrast was observed in Experiment 1. Possibly, the different gap durations (200 vs. 0 ms) explain the discrepancy (see "Discussion"). Further, latencies where 20 ms shorter with the dark than the light background (216 vs. 236), $F(1,17) = 5.3$, $p < 0.05$.

Background luminance and target contrast interacted significantly, $F(1,17) = 45.3$, $p < 0.001$, indicating that the slowing of RTs with low- compared to high-contrast targets was stronger on the light background (261 vs. 212 ms) than on the dark background (213 vs. 193 ms), $t(17) = 6.34$, $p < 0.001$. The latter difference of 20 ms is similar to the 17-ms effect of target contrast reported by Hunt and Kingstone (2003) which confirms that we closely replicated their stimulus display.

The IOR effect was of 36 ms, $F(1,17) = 87.8$, $p < 0.001$. Importantly, IOR was modulated by contrast, $F(1, 17) = 18$, $p = 0.001$, indicating larger IOR with low-contrast compared to high-contrast targets (43 vs. 30 ms). IOR was also considerably modulated by gap, $F(1,17) = 16.9$, $p = 0.001$, indicating less IOR with the step compared to the overlap condition (28 vs. 43 ms). Finally, there was also a significant four-way interaction, $F(4,68) = 3.6$, $p < 0.02$. To explore this interaction further, t tests (Bonferroni correction applied) were run. With the light background, IOR was greater when target contrast was low than when it was high, but only significantly so in the step condition (47 vs. 23 ms), $t(17) = 3.4$, $p < 0.05$, and not in the overlap condition (43 vs. 42 ms). On the dark background, IOR was significantly greater with low than high contrast in the overlap condition (57 vs. 31 ms), $t(17) = 4.3$, $p < 0.001$, but not in the step condition (22 vs. 19 ms).

Discussion

We tested the effect of variables thought to tap the perceptual/attentional or motor stages on IOR. Contrary to a previous report (Hunt and Kingstone 2003), we have found only little differences between ocular and manual responses. The following results will be discussed in turn:

1. Target contrast affected IOR with manual *and* saccadic responses.
2. The difference in IOR between low- and high-contrast targets decreased with increasing RT for saccades, but not manual responses (Fig. 2b), suggesting that the measure of central tendency and the range of allowable RTs are important parameters in the data analysis.
3. We found no effect of gap on IOR with saccadic responses in the first experiment, but did so in the second experiment.
4. Significant modulation of the gap effect by target contrast with the 0-ms gap (Exp. 2) but not with the 200-ms gap (Exp. 1) suggests an additional attentional component in the former condition.
5. Effects of gap and target contrast on IOR depended on background luminance.

Effect of target contrast

Many studies have suggested that saccadic IOR may be different from manual IOR. For instance, IOR was shown to affect locations in an environmental reference frame for key-press responses (Posner and Cohen 1984; Maylor and Hockey 1985), but in a retinotopic reference frame for oculomotor responses (Souto and Kerzel 2009; Abrams and Pratt 2000). Also, IOR with key-press but not with saccadic responses was observed for stimuli that do not reach the SC, such as isoluminant blue stimuli (Sumner et al. 2004). However, dissociation of oculomotor and manual IOR with respect to the attentional component seems implausible, because selective attention and the programming of eye movements are tightly coupled. We confirmed this coupling by showing that IOR was stronger for low-contrast targets that benefit more from signal enhancement than high-contrast targets. Further, the existence of a perceptual component in saccadic IOR was corroborated by a study reporting an IOR effect on temporal order judgments (Li and Lin 2002). The decreasing effect of target contrast on IOR with increasing saccadic reaction times may explain why target contrast was not found to interact with saccadic IOR in the study of Hunt and Kingstone (2003). Alternatively, it may be that Hunt and Kingstone's contrast values resulted in a difference between dim and bright targets that was too small to produce significant interactions. Remember that their dim, low-contrast target had a (rather high) contrast of 55% whereas our low-contrast target with the bright background had less than 10% contrast. However, we replicated the interaction of contrast and IOR in the second experiment with a similar range of contrasts as in their study.

We also expected IOR to be greater with saccades than with key-press responses, as saccadic programming is more strongly coupled to attention than manual responses in general, and because saccades are more specifically directed at

the cued location than key-presses. Indeed, we found significantly larger IOR with saccades compared to key-press responses, but this effect has not always been replicated (Pratt and Neggers 2008; Briand et al. 2000; Reuter-Lorenz et al. 1996).

Gap effect

The modulation of IOR by gap with choice key-press responses is surprising at first sight, as key-press responses were not directed at the cued location, and therefore should not be sensitive to the motor bias component. However, it has been shown that IOR can under some circumstances affect responses that do not target the cued location. In one study, subjects were asked to press a key in response to a centrally presented arrow. Responses were slower when the direction of the arrow corresponded to a formerly fixated location (Taylor and Klein 2000). It is unlikely that attention caused a deficit in the perception of one arrow direction or another. Rather, the previous saccade may have produced directional inhibition at the motor level.

Consistent with previous research (Kingstone and Klein 1993b; Reuter-Lorenz et al. 1991), Experiment 1 showed that the gap effect does not interact with target contrast, suggesting that the gap effect does not involve attention. On the other hand, there was an interaction between gap effect and target contrast in Experiment 2, which fails to replicate Hunt and Kingstone's (2003) results.

If the gap were to facilitate attention to the target, the gap effect is expected to be larger with dim than with high-contrast targets (the same rationale as for the effects of target contrast on IOR applies). Reuter-Lorenz et al. (1991) found no interaction of target luminance with the gap effect when using a 200-ms gap (replicated in our Experiment 1). The gap effect was also not modulated by requiring attention shifts to the periphery (Kingstone and Klein 1993b), which provides further evidence against the involvement of attention in the gap effect. However, a significant interaction between gap and target contrast was found when we used a step (0-ms gap, Experiment 2) instead of a 200-ms gap (Experiment 1). The motor-preparation account of the gap-effect states that there is advance preparation of the motor parameters when the fixation point disappears 200 ms before target onset (e.g. Rolfs and Vitu 2007). This does not hold for the step condition, because the target appears at fixation offset and no advance preparation is possible. Therefore, it does not seem implausible that the processes underlying the 200-ms gap effect are not identical to the processes underlying the 0-ms gap effect. These differences may explain why there was an interaction between gap and target contrast with a 0-ms gap, but not with a 200-ms gap. Finally, the strict independence of the gap effect from attention is not uncontested. Pratt et al. (2006) have

demonstrated that attention to the remaining or to the vanishing part of a cross can modulate the gap effect. Clearly, further research on the effect of gap duration and its interaction with target contrast is needed.

Further, there was an effect of gap on IOR with saccadic responses in Experiment 2 which is predicted by a motor bias account of IOR. However, it was not significant in Experiment 1. Previous studies show some inconsistencies with respect to this effect. Hunt and Kingstone (2003) found larger IOR in the overlap compared to the gap condition which we replicated in both background conditions of Experiment 2, but not in Experiment 1. Abrams and Dobkin (1994) found the opposite relation, larger IOR with the gap, consistent with the tendency that we observed in Experiment 1. A difficulty in deciding which result may be more trustworthy is that no *a priori* prediction was formulated. Further, no significant effect of gap on IOR was found in our first experiment, even though statistical power was slightly higher than in Experiment 2 ($N = 22$ vs. $N = 18$), suggesting again different underlying processes in the 200-ms and the 0-ms gap. Alternatively, the absence of an effect with a true gap (200-ms gap) on IOR may also indicate that the ocular component of IOR is not as important as previously thought (see Fecteau and Munoz 2006).

In previous studies, the interaction of gap and IOR was taken as evidence for a motor component in IOR. This reasoning rests on the assumption that the gap effect has a purely motor origin. The interaction of gap and target luminance in Experiment 2 casts doubts on this assumption, because it suggests that attention was involved in the gap effect, at least with the 0-ms gap. Because the presence of an interaction between gap and IOR in Experiment 2 goes with an attentional component in the gap effect, while the absence of an interaction between gap and IOR in Experiment 1 goes with the absence of an attentional component in the gap effect, we are reluctant to conclude that our experiments provide evidence for a motor component in IOR. When there was an effect of gap on IOR, the gap effect also reflected attentional components.

Effects of background luminance

A rather surprising result in Experiment 2 was that background luminance affected IOR. We expected very similar results on light and dark backgrounds. Contrary to our expectation, the effect of gap and target contrast on IOR changed as a function of background luminance. One may think that contrast polarity also plays a role in this interaction, as the polarity of our targets was opposite on light and dark backgrounds. On the light background, targets were darker than the background, whereas targets were lighter on the dark background (see Fig. 3). To our knowledge, response asymmetries between the ON and OFF pathway

(see Chichilnisky and Kalmar 2002), which contribute, respectively, to the detection of increments and decrements of light, do not provide grounds to expect an effect of target polarity on IOR. Further, Posner and Cohen (1984) reported no difference in IOR when the cues consisted of a dimming or a brightening. There is a well documented advantage of light decrements over increments in reaction times, but it is confined to situations where background luminance levels are below those reported here (Cao et al. 2007). Therefore, it seems more plausible to look for explanations in terms of effects of mean luminance, although an independent variation of background luminance and polarity should be run to confirm this later point. The recent dissociation between magnocellular and parvocellular pathways in IOR (Sumner et al. 2004) may shed some light on the effect of background luminance. There is evidence showing that the contrast response of parvo (P) cells is weaker with low background luminance than the contrast response of magno (M) cells. It is also known that the intermediate layers of the superior colliculus (SC) receive their main input from the M-pathway (Schiller and Malpeli 1977; Schiller et al. 1979). Sumner et al. (2004) have recently used this property to unveil attentional components of IOR by using isoluminant stimuli (optimal for S-cones) to which the M-pathway, and hence the SC, is blind. As measured in the lateral geniculate nucleus (LGN), the M-cell contrast response is higher and saturates at much lower background luminance levels than P-cells (Purpura et al. 1988). Thus, low luminance backgrounds promote the influence of the M-pathway, by silencing the P-pathway (to some extent), and thus may engage oculomotor structures like the SC and FEF more strongly than high luminance backgrounds. Even if the light and dark background luminance used here cannot fully dissociate the two contributions, they may strongly modulate their respective weights. Neurophysiological studies have shown that a decrease of activity of fixation cells of the rostral SC correlates with the gap effect (Dorris and Munoz 1995). As for IOR with manual responses, it has recently been shown that the gap effect occurs also for stimuli that bypass the M-pathway (Sumner et al. 2006), suggesting parallel contributions of M- and P-pathways to the effect. Altogether, this indicates that the use of a dark background may favor the expression of the oculomotor components in gap and IOR effects. However, the effects of gap on IOR are not stronger on a dark background. Further research is clearly needed to tease apart effects of background luminance from effects of target contrast or contrast polarity.

More practically, the finding that background luminance generates partly unpredictable differences in IOR raises some concerns about the replicability of effects associated with IOR. Looking at some of the studies relevant to the questions tackled in this paper, we noticed that the

background luminance varies greatly. The background luminance was on most occasions not reported (e.g. Abrams and Dobkin 1994; Gibson and Egeth 1994; Danziger and Kingstone 1999; Kingstone and Pratt 1999; Ro et al. 2000, 2003; Ivanoff and Klein 2006), even when details about the luminance of the stimuli were reported (e.g. Li and Lin 2002). Values of 0.15 cd/m^2 (Chelazzi et al. 1995; Berlucchi et al. 2000), possibly about the same as with a "black background" (Taylor and Klein 2000; Godijn and Theeuwes 2002), were also reported. A minority of studies used a light gray background, of 25 cd/m^2 (Sumner et al. 2004, 2006) similar to the one in our own experiments (29.5 cd/m^2). The use of a gray background, approaching normal daylight conditions, seems preferable in further experiments. At least, background luminance should be reported for the sake of comparability between studies.

Conclusion

Our finding that IOR measured with saccadic responses is affected by target contrast is in agreement with a large amount of evidence indicating that programming of saccades and spatial attention are closely coupled. Unexpectedly, we have found that relatively small variations in background luminance radically change the way gap and target contrast affect IOR. The differences possibly arise from the different contributions of the magnocellular and parvocellular pathways in the generation of IOR. We also fail to provide evidence for a motor component in saccadic IOR, which is consistent with recent proposals that IOR is mainly due to sensory/perceptual process.

References

Abrams RA, Dobkin RS (1994) The gap effect and inhibition of return: interactive effects on eye movement latencies. Exp Brain Res 98:483–487

Abrams RA, Pratt J (2000) Oculocentric coding of inhibited eye movements to recently attended locations. J Exp Psychol Hum Percept Perform 26:776–788

Bekkering H, Pratt J, Abrams RA (1996) The gap effect for eye and hand movements. Percept Psychophys 58:628–635

Berlucchi G, Chelazzi L, Tassinari G (2000) Volitional covert orienting to a peripheral cue does not suppress cue-induced inhibition of return. J Cogn Neurosci 12:648–663

Briand KA, Larrison AL, Sereno AB (2000) Inhibition of return in manual and saccadic response systems. Percept Psychophys 62:1512–1524

Cao D, Zele AJ, Pokorny J (2007) Linking impulse response functions to reaction time: Rod and cone reaction time data and a computational model. Vis Res 47:1060–1074

Carpenter RH, Williams ML (1995) Neural computation of log likelihood in control of saccadic eye movements. Nature 377:59–62

Chelazzi L, Biscaldi M, Corbetta M, Peru A, Tassinari G, Berlucchi G (1995) Oculomotor activity and visual spatial attention. Behav Brain Res 71:81–88

Chichilnisky EJ, Kalmar RS (2002) Functional asymmetries in ON and OFF ganglion cells of primate retina. J Neurosci 22:2737–2747

Danziger S, Kingstone A (1999) Unmasking the inhibition of return phenomenon. Percept Psychophys 61:1024–1037

Deubel H, Schneider WX (1996) Saccade target selection and object recognition: evidence for a common attentional mechanism. Vision Res 36:1827–1837

Dorris MC, Munoz DP (1995) A neural correlate for the gap effect on saccadic reaction times in monkey. J Neurophysiol 73:2558–2562

Fecteau JH, Munoz DP (2006) Salience, relevance, and firing: a priority map for target selection. Trends Cogn Sci 10:382–390

Fischer MH, Pratt J, Neggers SF (2003) Inhibition of return and manual pointing movements. Percept Psychophys 65:379–387

Gibson BS, Egeth H (1994) Inhibition and disinhibition of return: evidence from temporal order judgments. Percept Psychophys 56:669–680

Godijn R, Theeuwes J (2002) Oculomotor capture and inhibition of return: evidence for an oculomotor suppression account of IOR. Psychol Res 66:234–246

Hawkins HL, Shafto MG, Richardson K (1988) Effects of target luminance and cue validity on the latency of visual detection. Percept Psychophys 44:484–492

Heathcote A, Popiel SJ, Mewhort DJK (1991) Analysis of response time distributions: an example using the stroop task. Psychol Bull 109:340–347

Hunt AR, Kingstone A (2003) Inhibition of return: dissociating attentional and oculomotor components. J Exp Psychol Hum Percept Perform 29:1068–1074

Ignashchenkova A, Dicke PW, Haarmeier T, Thier P (2004) Neuron-specific contribution of the superior colliculus to overt and covert shifts of attention. Nat Neurosci 7:56–64

Ivanoff J, Klein RM (2006) Inhibition of return: sensitivity and criterion as a function of response time. J Exp Psychol Hum Percept Perform 32:908–919

Kingstone A, Klein RM (1993a) Visual offsets facilitate saccadic latency: does predisengagement of visuospatial attention mediate this gap effect? J Exp Psychol Hum Percept Perform 19(6):1251–1265

Kingstone A, Klein RM (1993b) What are human express saccades? Percept Psychophys 54:260–273

Kingstone A, Pratt J (1999) Inhibition of return is composed of attentional and oculomotor processes. Percept Psychophys 61:1046–1054

Li CS, Lin SC (2002) Inhibition of return in temporal order saccades. Vision Res 42:2089–2093

Luce RD (1991) Response times: their role in inferring elementary mental organization. Oxford University Press, New York

Machado L, Rafal R (2004) Inhibition of return generated by voluntary saccades is independent of attentional momentum. Q J Exp Psychol A 57:789–796

Maylor EA (1985) Facilitatory and inhibitory components of orienting in visual space. In: Posner MI, Marin OSM (eds) Attention and performance XI. Erlbaum, Hillsdale, NJ, pp 189–203

Maylor EA, Hockey R (1985) Inhibitory component of externally controlled covert orienting in visual space. J Exp Psychol Hum Percept Perform 11:777–787

Murray IJ, Plainis S (2003) Contrast coding and magno/parvo segregation revealed in reaction time studies. Vis Res 43(25):2707–2719

Posner MI, Cohen Y (1984) Components of visual orienting. In: Bouma H, Bowhuis D (eds) Attention and performance X. Erlbaum, Hillsdale, NJ, pp 531–556

Pratt J, Neggers B (2008) Inhibition of return in single and dual tasks: examining saccadic, keypress, and pointing responses. Percept Psychophys 70:257–265

Pratt J, Lajonchere CM, Abrams RA (2006) Attentional modulation of the gap effect. Vis Res 46(16):2602–2607

Purpura K, Kaplan E, Shapley RM (1988) Background light and the contrast gain of primate P and M retinal ganglion cells. Proc Natl Acad Sci USA 85:4534–4537

Rafal RD, Calabresi PA, Brennan CW, Sciolto TK (1989) Saccade preparation inhibits reorienting to recently attended locations. J Exp Psychol Hum Percept Perform 15:673–685

Ratcliff R (1979) Group reaction time distributions and an analysis of distribution statistics. Psychol Bull 86:446–461

Reuter-Lorenz PA, Hughes HC, Fendrich R (1991) The reduction of saccadic latency by prior offset of the fixation point: an analysis of the gap effect. Percept Psychophys 49:167–175

Reuter-Lorenz PA, Jha AP, Rosenquist JN (1996) What is inhibited in inhibition of return? J Exp Psychol Hum Percept Perform 22:367–378

Ro T, Pratt J, Rafal RD (2000) Inhibition of return in saccadic eye movements. Exp Brain Res 130:264–268

Ro T, Farne A, Chang E (2003) Inhibition of return and the human frontal eye fields. Exp Brain Res 150:290–296

Rolfs M, Vitu F (2007) On the limited role of target onset in the gap task: support for the motor-preparation hypothesis. J Vis 7(10):7, 1–20.

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

Schiller PH, Malpeli JG (1977) Properties and tectal projections of monkey retinal ganglion cells. J Neurophysiol 40:428–445

Schiller PH, Malpeli JG, Schein SJ (1979) Composition of geniculostriate input ot superior colliculus of the rhesus monkey. J Neurophysiol 42:1124–1133

Schmidt WC (1996) Inhibition of return is not detected using illusory line motion. Percept Psychophys 58:883–898

Sheliga BM, Riggio L, Rizzolatti G (1994) Orienting of attention and eye movements. Exp Brain Res 98:507–522

Sheliga BM, Riggio L, Rizzolatti G (1995) Spatial attention and eye movements. Exp Brain Res 105:261–275

Shepherd M, Findlay JM, Hockey RJ (1986) The relationship between eye movements and spatial attention. Q J Exp Psychol A 38:475–491

Smith DT, Rorden C, Jackson SR (2004) Exogenous orienting of attention depends upon the ability to execute eye movements. Curr Biol 14:792–795

Souto D, Kerzel D (2009) Involuntary cueing effects during smooth pursuit: facilitation and inhibition of return in oculocentric coordinates. Exp Brain Res 192:25–31

Spalek TM, Hammad S (2004) Supporting the attentional momentum view of IOR: is attention biased to go right? Percept Psychophys 66:219–233

Sternberg S (1969) The discovery of processing stages: extensions of Donders' method. Acta Psychol 30:276–315

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

Sumner P, Nachev P, Castor-Perry S, Isenman H, Kennard C (2006) Which visual pathways cause fixation-related inhibition? J Neurophysiol 95:1527–1536

Taylor TL, Klein R (1998) On the causes and effects of inhibition of return. Psychonomic Bull Rev 5:625–643

Taylor TL, Klein RM (2000) Visual and motor effects in inhibition of return. J Exp Psychol Hum Percept Perform 26:1639–1656

Tipples J (2002) Eye gaze is not unique: automatic orienting in response to uninformative arrows. Psychon Bull Rev 9:314–318

Welsh TN, Pratt J (2006) Inhibition of return in cue-target and target–target tasks. Exp Brain Res 174:167–175