

Research report

A perceptual level mechanism of the inhibition of return in oculomotor planning

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Abstract

A motor response to a visual target presented at a precued spatial location is facilitated if the target is presented shortly after the cue and inhibited when the cue target onset asynchrony approaches a few hundred milliseconds. The latter effect is termed inhibition of return (IOR). It is suggested that IOR provides an important strategy for effective search in our visual environment. Despite studies demonstrating IOR in a number of behavioral tasks, its neural mechanism has remained elusive. As a fundamental step toward understanding these mechanisms, the current study examines whether IOR mainly involves a perceptual or a motor process. We conducted a series of experiments, in which the target instructed saccades to the cued or to a different location. In each experiment, we observed a similar pattern of IOR when the target followed the cue, but not when the saccade was directed to the cued location. In another two experiments, we demonstrated that the magnitude and temporal profile of IOR varied depending on whether an eye movement or a manual response was involved. Overall, the present study suggests that IOR results predominantly from a perceptual level mechanism, with its magnitude and time course modulated by the activation of specific motor effectors. We discuss the implications of these results for attention gating of perceptual inputs and for mechanisms of visuomotor control. © 2002 Elsevier Science B.V. All rights reserved.

Theme: Neural basis of behaviour

Topic: Cognition

Keywords: Inhibition of return; Attention; Visual search; Oculomotor; Eye–hand coordination; Premotor theory

1. Introduction

Inhibitory mechanisms play an important role in human cognition [6,7]. When confronted simultaneously with hundreds of objects and events, for instance, we restrict our thoughts and actions to a subset of those that we might respond to. By voluntarily attending to the objects and events that are relevant to our immediate goals, we concurrently inhibit processing of those that are irrelevant. The selection process works bottom up as well. A transient onset in our perceptual space captures attention and processing resources. Studies over the years have described an inhibitory aspect of this selective attention—the

inhibition of return, or IOR, of attention [24]. It is suggested that, by directing attention away from a spatial location that has just been attended to, IOR provides an important behavioral strategy for effective foraging in our complex visual environment [15].

Fig. 1 illustrates the spatial cuing paradigm commonly used to demonstrate IOR in the laboratory. In the behavioral task, subjects fixate a center light to begin a trial. A peripheral cue then appears briefly either to the right or left of the fixation. After a random stimulus onset asynchrony (SOA), the center fixation extinguishes. At the same time, a target follows the cue at the same (valid trials) or at the opposite (invalid trials) location. Subjects make a rapid response to the target. In an experiment in which the cue does not predict the location of the target, as in the ones reported in this study, the motor response of the valid trials is facilitated at short SOAs and inhibited afterwards, compared to that of the invalid trials. Fig. 2a shows that saccade latencies of valid trials are shorter at

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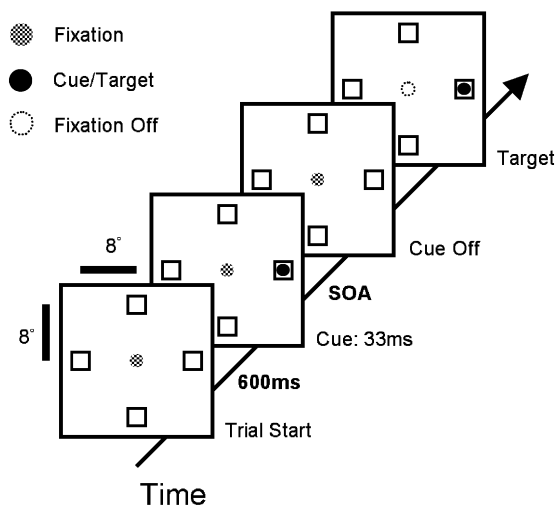


Fig. 1. Timing of events in all experiments. A pro-saccade task is illustrated here. A center fixation point appeared along with four square boxes at the beginning of each trial. A peripheral cue appeared briefly (33 ms) in one of the four boxes, after the subject acquired fixation for 600 ms. After a pseudorandomized SOA (67, 100, 150, 200, 400, 700 or 1200 ms), a target or imperative stimulus (a light spot, experiments 1–4, 6, 7; a center arrow, experiment 5) appeared in one of the four boxes (experiments 1–4, 6, 7) or replaced the central fixation light (experiment 5). The subjects had to maintain their eyes within a window of $1.2^\circ \times 1.2^\circ$ throughout fixation and make a saccadic eye movement/manual response as directed by the target within 500/750 ms after target onset.

SOAs around 67 ms and longer after, with the inhibition peaking at SOAs around 200 ms. This biphasic latency difference between valid and invalid trials has been consistently found in previous experiments on IOR [16].

What is inhibited in IOR? As was noted in earlier studies, IOR cannot be accounted for by low level sensory mechanisms [41]. First, it does not result from sensory masking, since IOR is longer lasting. Moreover, an inhibitory rather than facilitative effect should have been observed at a short SOA if masking were in operation. Second, IOR demonstrates interocular transfer, which would not be expected if the inhibition occurs at the level of retina [40]. And IOR can be observed with the cue and target presented in different sensory modalities [37]. Is it then a perceptual or a motor process? Or perhaps both of these mechanisms play a role in the generation of IOR?

The two hypothetical mechanisms differ with respect to the postulated level of inhibited information processing. The perceptual theory proposes that, as a result of disadvantaged attention, perceptual processing is inhibited at the cued location and IOR serves to prevent further orienting activities to the tagged location [25]. In contrast, the motor theory proposes that, as a result of the suppression of the orienting response elicited by the peripheral cue, motor responses toward the cued location are delayed [18,39]. Results obtained in a number of different paradigms have supported either a perceptual explanation of IOR [5,9,26,27] or a motor explanation [28,42] while still others have supported a mixed explanation [14,29].

Recent event-related potential (ERP) studies have also failed to yield any conclusive results with respect to this issue [10,11,20,21].

Evidence in favor of a perceptual mechanism came mainly from spatial cuing studies involving identity- or location-based discrimination. Correct discrimination rate or perceptual sensitivity instead of reaction time served as the dependent measure in these studies [5,9,26,27]. A major issue with a perceptual explanation is that it has not been able to address why IOR was not obtained in temporal order judgment or illusory line motion, which clearly were perceptual tasks [8,17,19,34]. As a matter of fact, the latter has often been cited as evidence supporting a motor mechanism of IOR [1,18,42]. Other results supporting a motor account derived from paradigms involving a semantic cue to direct the upcoming saccade (the ‘endogenous saccade task’). However, while some experiments demonstrated a significant IOR, others did not produce a consistent effect [1,29,42].

The current study attempts to address this issue on several fronts. First, few of the afore-mentioned experiments have directly contrasted the two possible explanations of IOR by evaluating the role of perceptual processing and motor preparation in a single behavioral task. Following Rafal et al., 1994 [29], the present study performs this direct comparison in a number of different paradigms that dissociate the directions of cue and target-directed saccade. Second, we repeat the endogenous saccade task, where a positive effect would clearly suggest an independent motor component in the generation of IOR. Third, by requiring the subjects to respond by eye and hand and solely by hand in two different experiments, we evaluate the contribution of different motor effectors to IOR. An important aspect of our study design is the wider range of cue target onset asynchronies employed in all of the experiments. This allows us to evaluate the IOR for an entire temporal profile instead of a single time point, which proves to be critical in assessing the contribution of perceptual and motor mechanisms to this inhibitory effect. Overall, we found IOR results from a predominantly perceptual mechanism whereas motor activation plays a modulatory role.

2. Materials and methods

2.1. Subjects, experimental setups and procedures

Ten (12) human subjects, 22 to 38 years of age and two of whom were the authors, participated in experiments 1 through 5 (6 and 7). All subjects have normal or corrected-to-normal vision. The experiments were carried out in a dark room, each divided into five blocks and carried out on separate days. Subjects were seated 50 cm in front of a ViewSonic P815 monitor, head stabilized with a chin rest. Eye positions were recorded with a video-based eyetracker

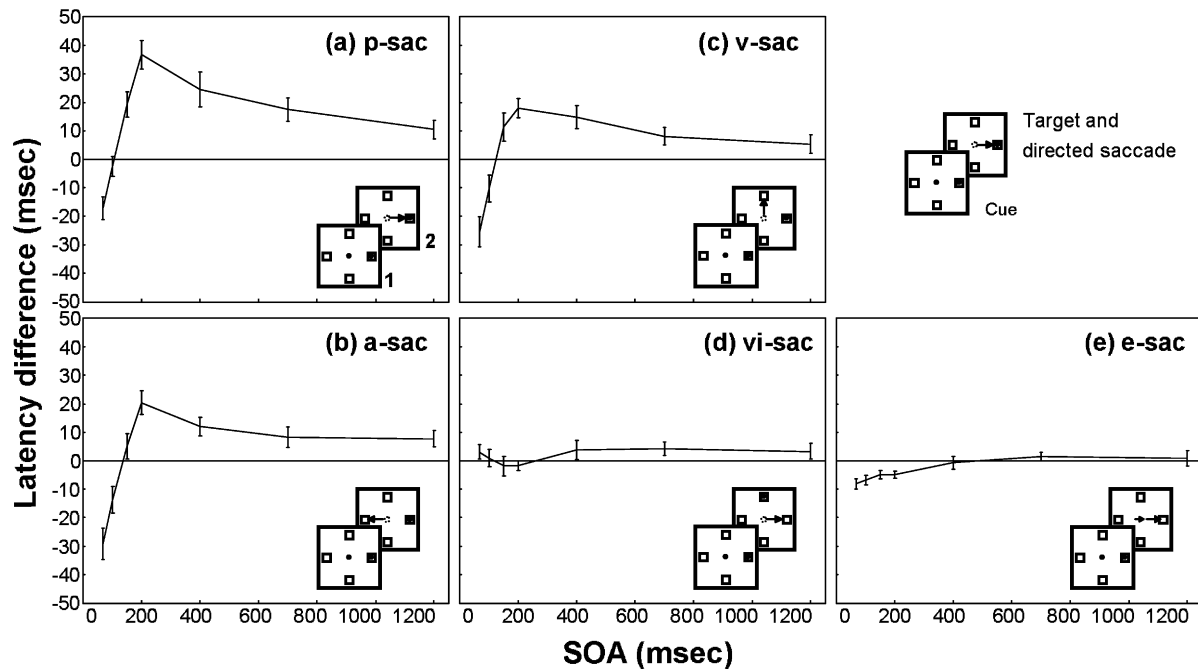


Fig. 2. Behavioral tasks and the temporal profile of IOR. Each data point represents at each SOA the difference between the median latencies of the valid and invalid trials in an experiment, averaged across the 10 subjects with standard error. A positive value indicates a longer latency for the valid trials. The data of rightward and leftward saccades were combined. The insets highlight the spatial relationship between cue (frame 1) and target-directed saccade (frame 2) in valid trials. In all tasks, the cue is neutral with respect to target location and saccade direction. (a) Pro-saccade task (p-sac). The cue and target appeared to the left or right of the fixation, at the same location in valid trials and opposite locations in invalid trials. The target commands a saccade to the cued location. The inhibition peaks at 200 ms. (b) Anti-saccade task (a-sac). As in the pro-saccade task, the cue and target appeared at the same location in valid trials and at opposite locations in invalid trials. However, the target instructs a saccade in the opposite direction—a target on the right signals a leftward saccade and vice versa. Nonetheless, a valid cue resulted in an early facilitation and a late inhibition of reaction time, exactly as in the pro-saccade task, even though the saccade was directed away from both cue and target. Moreover, the temporal profiles of inhibition are similar for pro- and anti-saccade tasks. (c) ‘Vertical’ saccade task (v-sac). The cue and target locations are the same as in the pro- and anti-saccade tasks. Now the target instructs an eye movement 90° off the cued direction: a right target commands an upward and a left target a downward saccade. The time course of inhibition again appears similar to that of the pro- and anti-saccade tasks. (d) ‘Vertically instructed’ saccade task (vi-sac). The target appeared in one of the boxes on the vertical axis, with an upper target signaling a rightward and a lower target a leftward saccade. The latency did not significantly differ between valid and invalid trials across the SOAs. (e) The ‘endogenous saccade’ task (e-sac). The cue locations are the same as in the pro-saccade task. At the time of target onset, a center arrow replaced the fixation light and served as the imperative stimulus, directing a saccade either to the right or to the left. No IOR is evident.

(Eyelink®, SR Research, Toronto, Canada) with a sampling rate of 250 Hz and a spatial resolution of 0.1°, and were corrected for head movement. Saccade onset was defined as the time when the eye movement velocity exceeded 30°/s. The visual stimuli were generated by a personal computer using VGA graphic card and displayed in synchrony with screen refresh at 60 Hz. The center fixation point was a circle 0.7° of visual angle in diameter and 4.6 cd/m² of luminance (Fig. 1). Each of the four square boxes was 0.8° across and 0.1 cd/m² of luminance and was located 8° of visual angle from the fixation. In all experiments, both cue and target were a circle 0.7° in diameter (target was an arrow 0.7° across in the endogenous saccade task) and 18.75 cd/m² of luminance. There were a total of 7 (SOA)×2 (direction)×2 (cue validity)×30 (repetitions)=840 trials in an experiment.

Subjects initiated a trial by pressing the space bar on the keyboard in experiments 1 through 5. For experiments 6 and 7, to obviate any possible interference with the manual

response, trial start was auto-triggered by eye fixation rather than manually timed by the subjects. A practice session was run before the experiment proper. The subjects were instructed that the cue does not predict the location of the target and that they should make a saccade/button press as directed by the target as rapidly as they could after target onset. The figure legends describe the details of the experimental paradigms.

2.2. Data analysis

The average error rate across all tasks and subjects is 3.67%. The trials with a saccade/manual response latency less than 100/150 ms were considered anticipatory and excluded from the analyses. A two-way (task×SOA) analysis of variance (ANOVA) with repeated measures was conducted for the statistical tests for all experiments, with the data of rightward and leftward saccades combined. The *P* values shown were the results of multivariate tests.

3. Results

The cued saccade (pro-saccade, experiment 1) task, in which the target presented at the cued location instructs a saccade toward the same eccentricity, does not distinguish between a perceptual and a motor process: the effect of the peripheral cue on the early processing of the target is confounded with its effect on the preparation and execution of a saccade toward the cued location (Fig. 2a). In other words, IOR could be observed either as a result of the target presented at the cued location or of the saccade made to the cued location. In order to dissociate the two components, we introduced a cued anti-saccade task with the target signaling the subject to make a saccade in the opposite direction (experiment 2). Comparing the results obtained in the pro- and anti-saccade tasks enabled us to distinguish whether a perceptual, a motor or perhaps both mechanisms led to IOR. The results largely supported the perceptual account (Fig. 2b). Although the overall inhibition was larger in the pro-saccade task ($P < 0.01$), the temporal profiles of inhibition did not differ between the two tasks ($P > 0.84$, task \times SOA interaction): the patterns of the latency difference were in the same direction when the cue was considered as cuing the location of the target as opposed to the end point of the saccade. Moreover, the peak magnitude of inhibition is significantly correlated between the pro-saccade and anti-saccades ($r^2 = 0.5149$, $P < 0.02$, Fig. 3a).

One might argue that, to execute an anti-saccade, our brain associates the sensory stimulus with an appropriate motor response—a sensorimotor transformation that does not easily allow one to determine where the sensory process ends and the motor mechanism starts [44]. Therefore, the observation of a similar pattern of inhibition in the cued anti-saccade task may not exclude a motor component in IOR.

To further investigate whether perceptual and motor mechanisms may each contribute to IOR, we engaged the same subjects in a second set of experiments. In one

(‘vertical saccade’, experiment 3) task, the target appeared on the horizontal axis, the right one commanding an upward and the left one a downward saccade (Fig. 2c). In this case, the target followed the cue at the same location in valid trials and the saccades were 90° off the direction of any motor activities the cue may have triggered. In the other (‘vertically instructed saccade’, experiment 4) task, the target appeared on the vertical meridian, the upper one signaling a rightward and the lower one a leftward saccade (Fig. 2d). In other words, although the target did not follow the cue at the same location, it directed the saccade to the cued location in valid trials. Since a motor response 90° off the direction of the sensory stimulus was instructed for both vertical and vertically instructed saccades, in contrast to the difference between pro- and anti-saccades, similar sensorimotor transformations are involved in these two tasks. A perceptual mechanism would be supported if IOR was observed in the vertical saccade task but not in the vertically instructed saccade task. Conversely, a motor mechanism would be supported if the opposite pattern of results was observed. If IOR were observed in both tasks, a mixture of both perceptual and motor mechanisms would be supported. The results showed that, although the overall magnitudes of latency difference were similar ($P > 0.71$), the temporal profiles differed between the two tasks ($P < 0.02$, task \times SOA interaction). A temporal pattern of inhibition, statistically indistinguishable from that observed in the pro-saccade task, was obtained in the vertical saccade ($P > 0.22$, task \times SOA interaction), but not in the vertically instructed saccade task ($P < 0.03$, task \times SOA interaction). Little latency difference was obtained between valid and invalid trials in the latter. And again, individual subjects showed a tight correlation in the peak magnitudes of inhibition between pro-saccades and vertical saccades ($r^2 = 0.5742$, $P < 0.02$, Fig. 3b). These experiments provide more evidence that a perceptual mechanism plays a dominant role in the generation of IOR.

As another attempt to explore whether any motor process might contribute to the generation of IOR, we

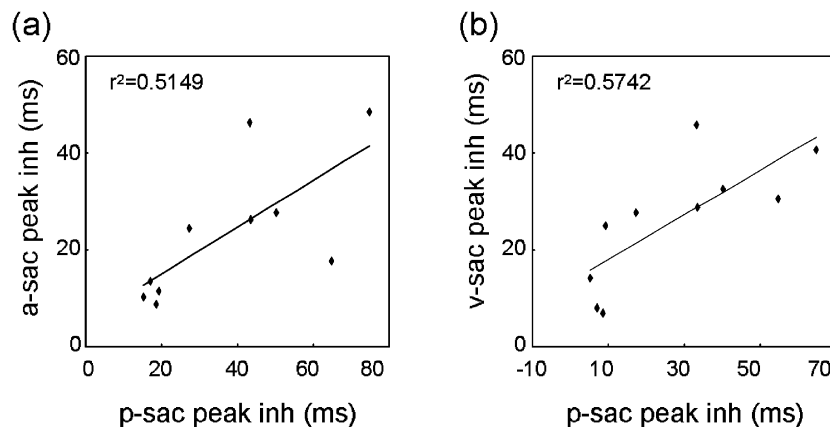


Fig. 3. Correlation of the peak magnitudes of IOR between the pro-saccades and anti-saccades (a) and between the pro-saccades and vertical saccades (b). Each point represents an individual subject.

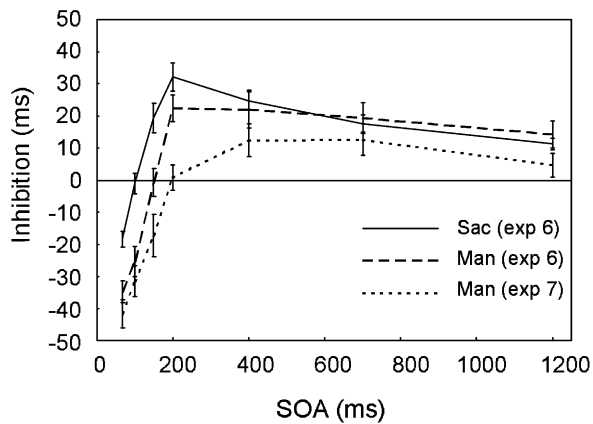


Fig. 4. IOR in saccade and manual response with and without an eye movement. Data are presented in the same format as in Fig. 2. Each line, connecting the means of the twelve subjects, shows the latency difference between valid and invalid trials for saccadic eye movements (solid line) and manual responses (coarse dashed line) in experiment 6, and for manual responses in experiment 7 (fine dashed line). See text for explanation and statistics.

conducted an experiment employing a central arrow to signal the saccade direction—the endogenous saccade task (experiment 5). Since the saccade was directed by the semantic meaning of the cue, rather than by an exogenous stimulus, the task was devoid of simple cue–target interaction at the perceptual level. A positive inhibitory effect would suggest the involvement of a motor process. The results revealed a virtually flat latency difference across the SOAs, again in support of a perceptual theory (Fig. 2e). It thus appears that endogenous motor process *alone* plays little role in the generation of IOR.

So far we have demonstrated that IOR results predominantly from an inhibition at the level of perceptual processing. Does motor process perhaps modulate the magnitude and time course of IOR? In particular, does oculomotor activation play a specific role in the generation of IOR? Experiments 6 and 7 evaluated these issues. In experiment 6 subjects made a manual response as well as a

saccade to the target in a ‘pro-saccade’ experiment. In experiment 7 they made a manual response to the target while holding their eyes at fixation. The visual display and cue and target timing were exactly the same as in the pro-saccade experiment. The results showed that when eye and hand movements were executed at the same time, both demonstrated an IOR (Fig. 4). Although the magnitude of IOR was significantly larger with saccades than with manual responses ($P < 0.005$), the time course was similar ($P > 0.12$, task \times SOA interaction). When eye movements were disallowed, manual response demonstrated an IOR with a smaller magnitude and a slower time course ($P < 0.016$, task; $P < 0.038$, task \times SOA interaction, comparing the manual responses in the two tasks, Fig. 4). Furthermore, the peak magnitude of inhibition is significantly correlated between the saccade and manual response in experiment 6 ($r^2 = 0.6417$, $P < 0.002$, Fig. 5a) but not between the manual responses in the two experiments ($r^2 = 0.2665$, $P = 0.09$, Fig. 5b). These results suggest that activation of different effectors does modulate the magnitude and time course of IOR and that a major component of IOR depends on eye movement.

4. Discussion

The current results suggest that the delay of a saccade to a cued location, a seemingly motor impairment, could be explained by a perceptual-level mechanism characterized by interactions between stimuli presented successively at the same spatial location. These results are fairly robust; IOR is evident when cue and target appear at the same location but not otherwise. Moreover, individual subjects demonstrate a significant and tight correlation in the peak magnitudes of inhibition either between the oculomotor tasks or between the eye and hand responses when the two effectors were activated concurrently. The correlation suggests that these behavioral tasks are rightly tapping the visuomotor mechanisms responsible for the occurrence of

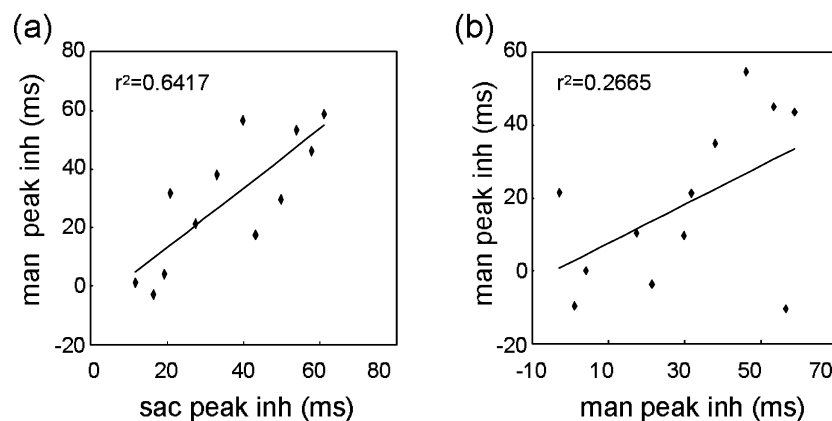


Fig. 5. Correlation of the peak magnitudes of IOR between the cued saccade and manual response in experiment 6 (a) and between the manual responses of experiments 6 and 7 (b). Each point represents an individual subject. Note the scales are different in the two plots.

IOR. The present result is consistent with earlier modeling studies which incorporated IOR in a saliency-based framework to account for the movement of attention in a perceptual space [12,13,19]. In such models a winner-take-all mechanism determines the focus of attention and IOR, embedded in this bottom-up structure, serves to transiently deactivate the focus and switches attention to the next most-conspicuous location.

The observation that the overall magnitude of inhibition is larger in the pro-saccade task than in the anti- and vertical saccade tasks may suggest a possible motor contribution. Nevertheless, the absence of IOR in the vertically instructed and endogenous saccade tasks indicates that, if any, this motor mechanism is contingent on the processing of an external stimulus presented at the cued location. It thus appears that, although motor activity spatially congruent with the imperative stimulus may augment the magnitude of IOR (as in pro-saccade vs. anti-saccade), activation of the motor process alone does not suffice to generate IOR. A perceptual mechanism mediated by the cue and target appearing at the same spatial locations is required.

Rafal et al. [29] employed an anti-saccade task to address the role of perceptual and motor mechanisms in IOR. They demonstrated that the latency of anti-saccade was longer than pro-saccade and that the latency of cued saccade was longer than uncued saccade, without significant interaction between task (pro- vs. anti-) and target location (cued vs. uncued). The study concluded that “the results are inconsistent with the notion that inhibition of return reflects only a motor alternation bias that favors saccades away from the precued location”, and that “this result is exactly what would be predicted if inhibition of return acted only by inhibiting detection of targets at the tagged location”.

The current study substantiated this finding and specified how perceptual and motor mechanisms each differentially contribute to IOR. By varying the cue target onset asynchronies over a wider time range, we showed that the temporal profiles of facilitation and inhibition were not different between pro- and anti-saccades. This result is important, as we now know that the temporal profile of IOR could vary depending on motor responses (experiments 6 and 7, current study; [3]) and other factors such as the luminance of the cue and target (Li and Lin, unpublished data). An anti-saccade task might as likely entail a different temporal profile of IOR, which could have been missed if only one or a few SOAs were sampled. Our results thus not only provide evidence for a role of a perceptual mechanism in IOR but also specifies how it works, in contrast to a motor mechanism, which appears to play a modulatory role.

Literature on the neural structures mediating IOR is relatively sparse. Earlier experiments suggested that lesions impairing the oculomotor structures in the midbrain but not those in the cortex resulted in a concurrent loss of

IOR [25]. A recent patient study also posited that the superior colliculus be involved [33]. How might the superior colliculus or other areas in the visuomotor pathway participate in the generation of IOR? Although the behavioral evidence has yet to be established, recordings from the superior colliculus and the parietal cortex suggested neurons in these cortical and subcortical areas show diminished activation to sequential presentation of stimuli [30,32,35,43]. By relating the time course of behavioral inhibition to the neuronal modulation by sequential stimulation, one could perhaps determine the relevance of these findings to IOR.

Consistent with a recent report [3], the present results indicate that the oculomotor circuitry plays a dominant role in the generation of IOR. The observation that the IOR associated with the manual response depends on whether a concurrent eye movement is made to the target raises interesting issues about eye and hand movement control. The cross-coupling of eye and hand movements has long been documented in psychophysical studies (see Ref. [4] for a review). Planning of one movement affects the execution of the other and vice versa. Recent physiological experiments have also identified brain areas containing neurons that are active both during eye and reaching movements [2,22,36,38]. It has been suggested that the coexistence of saccade and reach activity in the same brain areas facilitates eye–hand coordination. One finding is particularly interesting in light of the current results—while neurons in these ‘reach areas’ respond to a reaching movement, they encode the upcoming movement in eye-centered coordinate [2,38]. This observation suggests that common neural signals are driving hand and eye movements before they reach the frontal cortex for motor execution. Since eye and hand movements involve different premotor circuitries and effectors, similar IORs observed for eye and hand responses provide further evidence that this inhibitory effect occurs at a level prior to motor processing.

The results obtained in experiments 6 and 7 have an interesting implication for a perceptual account of IOR. It is mentioned earlier that one issue that a perceptual explanation of IOR has failed to address is that IOR has so far not been observed in temporal order judgment or line motion illusion [8,17,19,34]. Since the subjects responded manually in all previous studies, one wonders whether an IOR could be obtained if they are asked to respond by an eye movement. Further experiments are required to answer this question.

The observation that motor activation modulates IOR is not inconsistent with the premotor theory of attention, which stipulates that attention orienting is a premotor effect resulting from activation of the oculomotor circuitry [31]. However, oculomotor activation alone is not sufficient to generate IOR, suggesting that this *inhibitory* aspect of attentional orienting can be dissociated from eye movement control [23]. Although voluntary eye movement

remains an important strategy for shifting spatial attention, the current results provide evidence for an independent mechanism for attention gating. This gating mechanism mediates the interactions between features and objects in our visual environment and furnishes a bias about where to move our eyes from one moment to another. By altering activity of the motor machinery in a spatially selective manner, IOR provides an important means for efficient allocation of our processing resources.

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References

- [1] R.A. Abrams, R.S. Dobkin, Inhibition of return: effects of attentional cuing on eye movement latencies, *J. Exp. Psychol.: Hum. Percept. Perform.* 20 (1994) 467–477.
- [2] A.P. Batista, C.A. Buneo, L.H. Snyder, R.A. Andersen, Reach plans in eye-centered coordinates, *Science* 285 (1999) 257–260.
- [3] K.A. Briand, A.L. Larrison, A.B. Sereno, Inhibition of return in manual and saccadic response systems, *Percept. Psychophys.* 62 (2000) 1512–1524.
- [4] D.P. Carey, Eye–hand coordination: eye to hand or hand to eye?, *Curr. Biol.* 10 (2000) R416–R419.
- [5] M. Cheal, G. Chastain, D.R. Lyon, Inhibition of return in visual identification tasks, *Vis. Cognit.* 5 (1998) 365–388.
- [6] D. Dagenbach, T.H. Carr (Eds.), *Inhibitory Processes in Attention, Memory, And Language*, Academic Press, San Diego, CA, 1994.
- [7] F.N. Dempster, C.J. Brainerd (Eds.), *Interference and Inhibition in Cognition*, Academic Press, San Diego, CA, 1994.
- [8] B.S. Gibson, H. Egeth, Inhibition and disinhibition of return: evidence from temporal order judgments, *Percept. Psychophys.* 56 (1994) 669–680.
- [9] T.C. Handy, A.P. Jha, G.R. Mangun, Promoting novelty in vision: inhibition of return modulates perceptual-level processing, *Psychol. Sci.* 10 (1999) 157–161.
- [10] J.B. Hopfinger, G.R. Mangun, Reflexive attention modulates processing of visual stimuli in human extrastriate cortex, *Psychol. Sci.* 9 (1998) 441–447.
- [11] J.B. Hopfinger, G.R. Mangun, Tracking the influence of reflexive attention on sensory and cognitive processing, *Cogn. Affect. Behav. Neurosci.* 1 (1998) 56–65.
- [12] L. Itti, C. Koch, A saliency-based search mechanism of overt and covert shifts of visual attention, *Vision Res.* 40 (2000) 1489–1506.
- [13] L. Itti, C. Koch, Computer modeling of visual attention, *Nat. Rev. Neurosci.* 2 (2001) 194–203.
- [14] A. Kingstone, J. Pratt, Inhibition of return is composed of attentional and oculomotor processes, *Percept. Psychophys.* 61 (1999) 1046–1054.
- [15] R.M. Klein, Inhibitory tagging system facilitates visual search, *Nature* 334 (1988) 430–431.
- [16] R.M. Klein, Inhibition of return, *Trends Cogn. Sci.* 4 (2000) 138–147.
- [17] R.M. Klein, W.C. Schmidt, Disinhibition of return: unnecessary and unlikely, *Percept. Psychophys.* 60 (1998) 862–872.
- [18] R.M. Klein, T.L. Taylor, Categories of cognitive inhibition with reference to attention, in: D. Dagenbach, T.H. Carr (Eds.), *Inhibitory Processes in Attention, Memory, And Language*, Academic Press, San Diego, CA, 1994, pp. 113–150.
- [19] C. Koch, S. Ullman, Shifts in selective visual attention: towards the underlying neural circuitry, *Hum. Neurobiol.* 4 (1985) 219–227.
- [20] E.A. Maylor, Facilitatory and inhibitory components of orienting in visual space, in: M.I. Posner, O.S.M. Marin (Eds.), *Attention and Performance XI*, Erlbaum, Hillsdale, NJ, 1985, pp. 189–203.
- [21] J.J. MacDonald, L.M. Ward, K.A. Kiehl, An event-related brain potential study of inhibition of return, *Percept. Psychophys.* 61 (1999) 1411–1423.
- [22] H. Mushiaki, N. Fujii, J. Tanji, Visually guided saccade versus eye–hand reach: contrasting neuronal activity in the cortical supplementary and frontal eye fields, *J. Neurophysiol.* 75 (1996) 2187–2191.
- [23] M.I. Posner, Orienting of attention, *Quart. J. Exp. Psychol.* 32 (1980) 3–25.
- [24] M.I. Posner, Y. Cohen, Components of visual orienting, in: H. Bouma, D. Bouwhuis (Eds.), *Attention and Performance X*, Lawrence Erlbaum, London, 1984, pp. 531–556.
- [25] M.I. Posner, R.D. Rafal, L.S. Choate, J. Vaughan, Inhibition of return: neural basis and function, *Cogn. Neuropsychol.* 2 (1985) 211–228.
- [26] J. Pratt, R.A. Abrams, Inhibition of return in discrimination tasks, *J. Exp. Psychol. Hum. Percept. Perform.* 25 (1999) 229–242.
- [27] J. Pratt, A. Kingstone, W. Khoe, Inhibition of return in location- and identity-based choice decision tasks, *Percept. Psychophys.* 59 (1997) 964–971.
- [28] R.D. Rafal, P.A. Calabresi, C.W. Brennan, T.K. Sciolto, Saccade preparation inhibits reorienting to recently attended locations, *J. Exp. Psychol. Hum. Percept. Perform.* 15 (1989) 673–685.
- [29] R. Rafal, R. Egly, D. Rhodes, Effects of inhibition of return on voluntary and visually guided saccades, *Can. J. Exp. Psychol.* 48 (1994) 284–300.
- [30] G. Rizzolatti, R. Camarda, L.A. Grupp, M. Pisa, Inhibitory effect of remote visual stimuli on visual responses of cat superior colliculus: spatial and temporal factors, *J. Neurophysiol.* 37 (1974) 1262–1275.
- [31] G. Rizzolatti, L. Riggio, B.M. Sheliga, Space and selective attention, in: C. Umiltà, M. Moscovitch (Eds.), *Attention and Performance XV*, MIT Press, Cambridge, MA, 1994, pp. 231–265.
- [32] D.L. Robinson, E.M. Bowman, C. Kertzman, Covert orienting of attention in macaques. II. Contributions of parietal cortex, *J. Neurophysiol.* 74 (1995) 698–712.
- [33] A. Sapir, N. Soroker, A. Berger, A. Henik, Inhibition of return in spatial attention: direct evidence for collicular generation, *Nat. Neurosci.* 2 (1999) 1053–1054.
- [34] W.C. Schmidt, Inhibition of return is not detected using illusory line motion, *Percept. Psychophys.* 58 (1996) 883–898.
- [35] L.H. Snyder, A.P. Batista, R.A. Andersen, Change in motor plan, without a change in the spatial locus of attention, modulates activity in posterior parietal cortex, *J. Neurophysiol.* 79 (1998) 2814–2819.
- [36] L.H. Snyder, A.P. Batista, R.A. Andersen, Saccade-related activity in the parietal reach region, *J. Neurophysiol.* 83 (2000) 1099–1112.
- [37] C. Spence, J. Driver, Auditory and audiovisual inhibition of return, *Percept. Psychophys.* 60 (1998) 125–139.
- [38] V. Stuphorn, E. Bauswein, K.P. Hoffmann, Neurons in the primate superior colliculus coding for arm movements in gaze-related coordinates, *J. Neurophysiol.* 83 (2000) 1389–1399.
- [39] G. Tassinari, S. Aglioti, L. Chelazzi, C.A. Marzi, G. Berlucchi, Distribution in the visual field of the costs of voluntarily allocated attention and of the inhibitory after-effects of covert orienting, *Neuropsychologia* 25 (1987) 55–71.

- [40] G. Tassinari, G. Berlucchi, Sensory and attentional components of slowing of manual reaction-time to non-fixated visual targets by ipsilateral primes, *Vision Res.* 33 (1993) 1525–1534.
- [41] T.L. Taylor, R.M. Klein, On the causes and effects of inhibition of return, *Psychon. Bull. Rev.* 5 (1998) 625–643.
- [42] T.L. Taylor, R.M. Klein, Visual and motor effects in inhibition of return, *J. Exp. Psychol. Hum. Percept. Perform.* 26 (2000) 1639–1656.
- [43] R.H. Wurtz, B.J. Richmond, S.J. Judge, Vision during saccadic eye movements. III. Visual interactions in monkey superior colliculus, *J. Neurophysiol.* 43 (1980) 1168–1181.
- [44] M. Zhang, S. Barash, Neuronal switching of sensorimotor transformations for antisaccades, *Nature* 408 (2000) 971–975.