

## Inhibition of return in perception and action

Erik Chang and Tony Ro

*Department of Psychology, Rice University, Houston, TX, USA*

Inhibition of return (IOR) refers to the delay in responses to previously cued locations. Whether IOR influences perceptual and/or motor processes has been controversial. To determine IOR effects on perception and action, this study examined IOR in spatially directed hand reaching (Experiment 1) and spatial localization of targets with a mouse cursor (i.e., an indirect visuomotor mapping/perceptual task; Experiment 2). The reaction times showed delayed responses for targets appearing within the whole cued hemifield for both tasks. However, hypometric spatial biases were consistently found only with directed reaching. Spatial biases in the mouse localization task were indirectly influenced by IOR and distinct from those in the reaching task. The dissociation in spatial characteristics for directed reaching vs. perception suggests that the effects of IOR are task dependent, but may be more directly linked to the dorsal motor system.

Inhibition of return (IOR) refers to the delay and decrease in correct responses to events occurring in overtly or covertly attended locations (Posner & Cohen, 1984; Posner, Rafal, Choate, & Vaughan, 1985; Rafal, Calabresi, Brennan, & Sciolto, 1989). IOR has been suggested to be evolutionarily significant, for it facilitates foraging in novel locations (Klein, 1988; Klein & MacInnes, 1999; Snyder & Kingstone, 2000; Theeuwes & Godijn, 2002). Since its initial discovery, the processes that IOR has been suggested to influence have been controversial (see Klein, 2000, for a comprehensive review; and Taylor & Klein, 1998). In brief, the theoretical approaches to the influences of IOR mainly comprise two hypotheses: Attentional-perceptual and motor.

The attentional-perceptual hypothesis holds that IOR is an attentional bias through which we sample novel locations and avoid the re-inspection of already-attended-to portions of objects and space. Under this account IOR is viewed as a mechanism in opposition to attentional orienting, and has been demonstrated to influence perceptual processing in opposite ways from attention, such as

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Please address all correspondence to: E. Chang or T. Ro, Department of Psychology—MS25, Rice University, PO Box 1892, Houston, TX 77251-1892, USA. Email: [auda@rice.edu](mailto:auda@rice.edu) or [tro@rice.edu](mailto:tro@rice.edu)

impairing target detectability and discrimination (Handy, Jha, & Mangun, 1999; Lupiáñez, Milan, Tornay, Madrid, & Tudela, 1997). It has also been found that IOR is associated with the reduction in magnitudes (McDonald, Ward, & Kiehl, 1999) or the delay (Prime & Ward, 2004) of certain ERP components. The reduction of the P1 component and the delay of the target-locked rather than the response-locked lateralized readiness potential indicate that IOR at least partly involves suppression of sensory-perceptual processing. IOR, however, has not been consistently found in tasks assessing the speed and accuracy of perceptual processing, including temporal order judgments (Maylor, 1985; Posner et al., 1985; but see Li & Lin, 2002), illusory line motion (Schmidt, 1996), and some nonspatial discrimination tasks<sup>1</sup> (Tanaka & Shimojo, 1996; Terry, Valdes, & Neill, 1994). The inconsistent influences of IOR on these perceptual tasks make the attentional-perceptual hypothesis unlikely to be the only account of the processes modulated by IOR.

The motor hypothesis has been advanced in several forms, but they all link the causes (Chelazzi, Biscaldi, Corbetta, Peru, Tassinari, & Berlucchi, 1995; Rafal et al., 1989) or effects (Berlucchi, Tassinari, Marzi, & DiStefano, 1989; Fuentes, Vivas, & Humphreys, 1999; Klein & Taylor, 1994; Tassinari, Aglioti, Chelazzi, Marzi, & Berlucchi, 1987) of IOR to motor or response processes. On the issue of its effects, IOR has been suggested to: (1) Suppress responses towards the cued hemifield (Berlucchi et al., 1989; Ro, Pratt, & Rafal, 2000; Tassinari et al., 1987), (2) change the criterion for responding to targets at the cued location (Taylor & Klein, 2000), or (3) inhibit the connection between a stimulus and its response (Fuentes et al., 1999). Here we will highlight two lines of evidence regarding the effects of IOR on motor processes that are most relevant to the current study.

First, it has been established that reaction times are affected not only at the validly cued location, but also at other positions on the same side of the visual field as the cue (Berlucchi et al., 1989; Tassinari et al., 1987). This “meridian effect” is regarded as an indirect piece of evidence supporting the motor hypothesis because it is consistent with the specification of direction with priority over distance in motor programs (Rizzolatti, Riggio, Dascola, & Umiltà, 1987; Rosenbaum, Inhoff, & Gordon, 1984). This priority of direction over distance, according to this account, produces similar effects of cues on targets appearing on the same side/direction as the cue than for cues and targets appearing on opposite sides of fixation.

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<sup>1</sup> Nonspatial discrimination tasks refer to discrimination tasks that do not involve target localization. For example, discriminations of Vernier offset, size change, luminance, colour, orientation, or form are all nonspatial. Tanaka and Shimojo (1996) found facilitation of return (FOR) for nonspatial discrimination tasks and IOR for those based on target localization, and they suggested that this dissociation corresponds with the neurophysiological distinction between the ventral (“what”) and dorsal (“where”) pathways.

Second, there is evidence showing that IOR influences not only reaction times and error rates, but also spatial characteristics of eye and hand movements. For example, Ro et al. (2000) demonstrated the spatial effects of IOR on saccadic eye movements. In that study, saccadic eye movement responses were made to previously cued or uncued locations. IOR was present in the saccadic latencies, but more importantly, the spatial characteristics of saccades were also biased by IOR; saccades were more hypometric (shorter) when the target appeared in the previously cued hemifield than when the target appeared in the uncued hemifield. In related studies investigating hand movements, Tipper, Howard, and Houghton (1998) examined IOR in a reaching task, measuring both reaction times (RTs) and the path of reaching in a modified IOR task. They not only found the signature pattern of IOR in RTs, but also showed that when lateralized cues preceded targets, reaching paths were biased toward the cue location in invalid trials (also see Howard, Lupiáñez, & Tipper, 1999). In both of these reaching studies, however, it was unclear how reaching paths were biased when the cue and target were at the same location because analyses were not reported for these conditions.

Although the spatial characteristics of saccades and hand movements have been shown to be influenced by IOR, it remains unclear in all of these studies examining spatial characteristics of movements whether the altered saccades and reaches were secondary to the effects on attention/perception or stemmed directly from effects on the motor system. One way to dissociate the influences of IOR on attentional-perceptual and motor processes is to examine if similar patterns of hypometric spatial biases as measured with saccades (Ro et al., 2000) can be observed in other motor systems, as well as in perception. If spatial biases in different motor systems and in perception are similar, the simplest account would be that IOR influences a supramodal spatial map that is subsequently used for both perceptual and motor processes. In contrast, if spatial biases vary across different motor systems and across motor and perceptual tasks, the most reasonable account would be that IOR differentially influences perception and different types of actions depending on the nature of the task. Finally, it could be that IOR has similar effects across different motor systems, but these effects differ from those on perception. In any of these cases, the nature of these differential spatial biases would be informative regarding the site(s) of IOR.

The current study was designed to determine whether IOR influences spatially directed reaching and whether the influences on the motor system may be independent from perception (cf. Ro, Rorden, Driver, & Rafal, 2001). The first experiment uses stimulus configurations similar to those of Experiment 2 in Ro et al. (2000), but instead of making saccades, the participants reached toward the target position with their right index fingers and without visual feedback of their finger position. With this design, we are able to examine both spatial and temporal characteristics of reaching toward the validly and invalidly cued locations. The main aim of Experiment 1 is to test the validity of the motor

hypothesis of IOR by contrasting the temporal and spatial characteristics of this experiment with those in Ro et al. (2000). If IOR has direct effects on motor processes, we might expect that spatial characteristics of reaching are subjected to inhibition in a way similar to those of saccades in Ro et al. (2000) and different from the way IOR modulates perception. To examine the influence of IOR on perception, Experiment 2 adopted a stimulus configuration that was the same as Experiment 1, but required participants to indirectly localize target locations with a mouse cursor. Because precision of localization was emphasized and the mouse cursor was visible when it was moved, performance on this task should heavily reflect participants' perception of the target location rather than the indirect physical movements of the mouse. We predict that the biases in perceived location should differ from those in the first experiment with reaching and in saccades (Ro et al., 2000). The dissociation between the spatial characteristics of a motor task (Experiment 1) and a perceptual task (Experiment 2) will provide further evidence regarding the influences of IOR on perception and action.

## EXPERIMENT 1: IOR IN HAND-REACHING

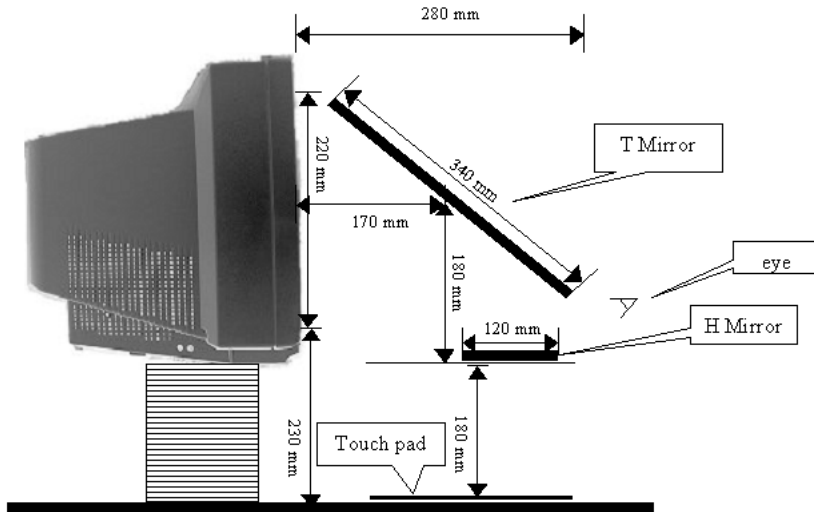
### Methods

#### *Participants*

After informed consent, following the guidelines according to the declaration of Helsinki and approval by the institutional review board of Rice University, 18 participants (8 males and 10 females) were recruited from the Rice University campus and participated for partial fulfilment of a course requirement (mean age: 19.27, range: 18–23). All subjects were right-handed and performed this task with their right hand. Data from two of them (one male) were discarded due to high overall error rates (41% and 81%, arising from long reaction times or long durations of movements).

#### *Apparatus*

*Image projection.* In order to avoid visual feedback from hand movements during the reaching task, a custom device was designed to present the stimuli. The stimuli were generated by a PC connected to a Sony Trinitron Multiscan 220GS monitor. The image from the monitor was projected onto a horizontal mirror (H mirror) placed in front of the subjects via another mirror (T mirror) that was tilted toward the monitor (see Figure 1). The size of the T mirror was 340 mm × 320 mm (width × height). The size of the H mirror was 340 mm × 120 mm. Both mirrors were 2 mm thick, front surface mirrors that were aluminized on the surface nearest the incident light (Sycamore Glass Components, Inc). Light was reflected without passing through any glass, and light loss (94% reflectance) and secondary refraction were minimized.



**Figure 1.** Apparatus for Experiment 1: See text for specifications of each component.

The T mirror was suspended by a custom-made wooden frame. The upper edge of the frame measured 27 cm vertically from the horizontal plane of the H mirror and formed a  $52^\circ$  angle against the vertical surface of the monitor. The lower edge of the T mirror was 9 cm vertically above the plane of the H mirror. The centre of the T mirror was in turn 18 cm vertically away from the plane of the H mirror, and 17 cm horizontally away from the centre of the monitor.

Participants were seated and looked at the images in the H mirror from a distance of approximately 15–20 cm, depending upon their height. A previous study found that restricting head movements with a chinrest impaired pointing accuracy (Biguer, Jeannerod, & Prablanc, 1985). The subjects' movements were therefore not restricted during the experiment, as long as they could see the image from the required distance and could move their right hand within the space formed by the device. The distance between the participants' eyes and the projected image of the stimuli from the monitor via the T mirror was 50 cm on the average. The H mirror was supported by a wooden shelf, and a touchpad (Elo touchsystems IntelliTouch<sup>®</sup> E281-2310) was placed beneath it. The touchpad was operated at a 9600 baud rate and had a temporal sampling rate of 100 Hz. The space under the mirror was large enough (18 cm high  $\times$  39 cm wide  $\times$  27 cm deep) for participants to move their hand, which they could not see, freely within a range approximately equal to the width of the monitor.

*Dynamic tracking.* A Polhemus FASTRACK<sup>®</sup> 3SPACE<sup>®</sup> tracking system (Polhemus, Inc.) was used to record the properties of movements. It uses electromagnetic fields to determine the position (x, y, and z coordinates) and

orientation (yaw, roll, and pitch) of a remote object (e.g., the hand). The electromagnetic field was generated by a transmitter (a plastic box containing coils) where the origins of all axes were located. In the experiment, the transmitter was on the same plane as the touchpad and fixed to the left of the participants. It was oriented such that the x-axis of the magnetic field was parallel to the main axis of hand-reaching (the azimuth (left–right) axis of the participant).

The position of the receiver indicating the finger position was calculated by the Polhemus central processing unit and sent to the main computer via the serial port. We used a single receiver so that the tracking system operated and was sampled by the computer at its maximum update rate of 120 Hz. The receiver was attached to the participant's right index finger and its movement was tracked through space and time.

### *Stimulus and procedures*

The stimulus display consisted of a black background. The fixation point, cues, and targets were all solid white dots that measured  $0.33^\circ$  of visual angle in diameter, when viewed at the projected distance of 50 cm. There were four possible locations of the cue and target. All of them, as well as the fixation dot, were located on the horizontal meridian. The fixation dot was located at the centre of the H Mirror. The near-target locations were located  $4^\circ$  to the right or left of fixation, whereas the far-target locations were located  $12^\circ$  from fixation in either hemifield. On the touchpad, the physical distance measured 3.5 cm and 10.5 cm from fixation to the near target and the far target, respectively.

At the beginning of the experiment, there was a calibration session in which the fixation point and the four possible target locations were presented. The participants were asked to position their right index finger at fixation and then to reach and touch each of the four peripheral locations one after another. The position of their unseen finger was shown to them through the projection system, using a small white dot with the text "Your position" beneath it, and participants were able to modify their finger position so that they managed to reach a spatial window of  $5 \times 5$  pixels ( $0.275^\circ \times 0.275^\circ$ ) around the target. The calibration sessions were repeated three times to allow participants to become familiar with how far their finger should go for each of the four target positions. In neither the practice nor test sessions was the location of the finger shown after the finger was positioned at fixation (i.e., the starting position). The deprivation of visual feedback served to eliminate the necessity for visuomotor integration.

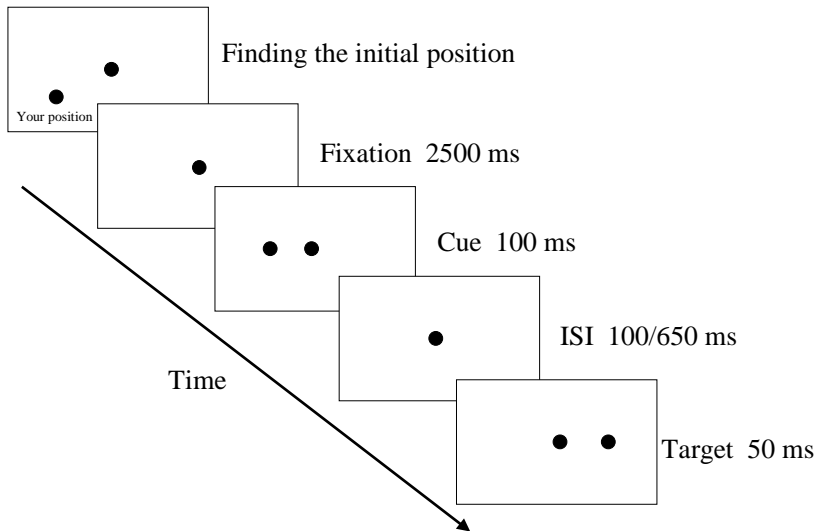
Every participant finished at least 10 practice trials, depending on how fast the task was mastered. In both the practice and test sessions, each trial began with the appearance of the fixation dot that remained on the display until the target was erased. Participants were instructed to position their finger on the location corresponding to the fixation dot on the touchpad. During this phase,

their position of contact was shown to help them reach the starting point. Once they reached the correct location, they were asked to hold their finger on that location and wait for the following events. After 2500 ms, the cue appeared at one of the four possible locations for 100 ms and then the target appeared after a 100 ms or 650 ms interstimulus interval (ISI) and remained present for 50 ms. The SOAs used were therefore 200 and 750 ms. The participants were asked to ignore the cue and make a speeded reach to the location of the flashed target by touching the corresponding position on the touchpad (see Figure 2).

### *Design*

For each target location, the spatial relationship between the cue and the target could be valid, within the same hemifield (called “within” hereafter), or between different hemifields (called “opposite-near” and “opposite-far”, depending on the cue’s eccentricity). In the valid condition, the cue and target appeared at the same location. In the within-hemifield condition, the target appeared  $8^\circ$  away from the cue, but both the cue and target were on the same side of the vertical meridian. In the opposite-hemifield conditions, the target could appear  $8^\circ$ ,  $16^\circ$ , or  $24^\circ$  away from the cue on the opposite side of the vertical meridian.

Within each cueing condition, half of the targets were at  $4^\circ$  of eccentricity and the other half at  $12^\circ$  of eccentricity, with the target appearing with equal



**Figure 2.** The schematic illustration of events presented in a typical trial for Experiment 1.

probability to the left or to the right of fixation. In addition, half of the trials were of the 200 ms cue–target SOA and the other half were of the 750 ms SOA. Thus, there were 24 trials for each of the 4 levels of cueing  $\times$  2 levels of target eccentricities  $\times$  2 levels of SOA, which totalled 384 trials for every participant.

### *Data analyses*

The dependent measures were reaction time (RT), movement time (MT), movement amplitude (MA), and endpoint of movement (EOM). RT was defined as the duration from the onset of the target to the initial release of the index finger from the touchpad. MT measured the duration from when the right index finger left the touchpad until it landed again on the touchpad. MA was extracted from the data registered by the magnetic tracking system and was computed in the following way. Immediately after the initiation of every reach, the position of the receiver was monitored until the touchpad was contacted. Because the movement was primarily along the left–right (x) axis, only the x-axis data were analysed. The position data were first smoothed by averaging across the adjacent five data samples for each data sample. Movement amplitude was then defined as the distance between the point at which the velocity exceeded 3 cm/s to where it fell below 3 cm/s. Movement amplitude is a measure of the spatial characteristic of hand movements, analogous to the saccadic amplitude measure as reported by Ro et al. (2000), and is a purer measure of movement extent because it does not include the fine motor adjustments typically made towards the end of reaching. The EOM was defined as the distance between the initial finger position and the first position where the subject's finger contacted the touchpad after the reach. EOM included the last, fine-adjustment phase of reaching toward the target. Again, we only analysed the x-axis data because the y-axis data variance was minimal in the current task. The values of the x-axis data were transformed from number of pixels to visual angles.

All dependent measures were subjected to a 4 (cueing: Cued, within, opposite-near, and opposite-far)  $\times$  2 (SOA: 200 and 750 ms)  $\times$  2 (target eccentricity: 4° and 12°) repeated measures ANOVA. Linear contrasts were used for post hoc comparisons. A trial would be regarded as an error if its RT was shorter than 100 ms or longer than 1000 ms, or if its MT was shorter than 100 ms or longer than 1500 ms. The RT and MT error rates were calculated for every condition and subjected to ANOVAs with the same design as the ANOVAs conducted on the other dependent variables. Error trials, however, were excluded from the main analyses of other dependent variables. A participant's data would not be included in the analysis if his/her overall error rate exceeded 20% (two subjects).



## Results

*Reaction time (RT).* The mean RTs across subjects for each condition are listed in Table 1. The RTs showed the signature pattern of IOR; that is, the cueing main effect was significant,  $F(3, 45) = 11.28, p < .001$ . RTs were longest in the valid condition, followed by the within condition, the opposite-far condition, and finally the opposite-near condition. The linear contrasts showed significant differences between the valid (599 ms) and the opposite conditions (577 ms),  $F(1, 15) = 18.98, p < .001$ , and between the valid and the within (589 ms) conditions,  $F(1, 15) = 5.63, p < .03$ . Figure 3 shows the RTs from the different cueing conditions for only the 750 ms SOA, when IOR is typically more robust and for more direct comparisons with Experiment 2, which only used a 750 ms SOA.

To examine whether there was a meridian effect, only the RTs of conditions with the same cue–target distance (i.e., the within and the opposite-near conditions for the near targets) were subjected to the linear contrast to avoid the confounding of a cue–target distance effect.<sup>2</sup> At the 200 ms SOA, the linear contrast between the within (615 ms) and the opposite-near condition (597 ms) for the near target was significant,  $F(1, 15) = 5.65, p < .03$ . At the 750 ms SOA, the within (552 ms) condition also had significantly longer RTs than the opposite-near condition (528 ms),  $F(1, 15) = 4.89, p < .04$ . The meridian effect in IOR, with longer RTs to targets at a location different from the cue but within the same hemifield, was thus measured and replicated (Berlucchi et al., 1989).

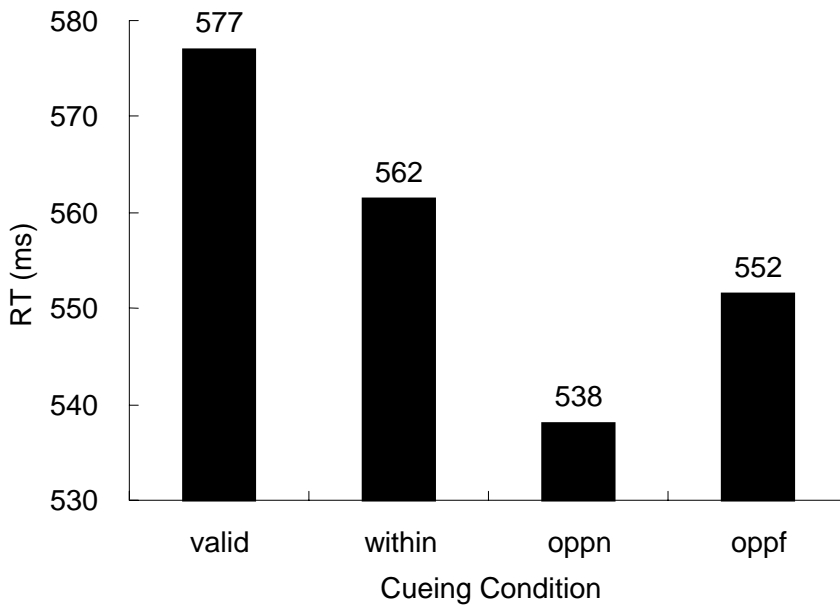
The main effect of SOA was highly significant,  $F(1, 15) = 110.38, p < .001$ . The RTs at the short SOA (614 ms) were longer than the RTs at the long SOA (557 ms). This effect is likely due to an alerting effect, with longer SOAs allowing better preparation for responding to targets (Posner & Boies, 1971). The effect of target eccentricity was also significant,  $F(1, 15) = 9.53, p < .01$ . The RTs to the near targets (579 ms) were shorter than the RTs to the far targets (593 ms). None of the interactions were significant (all  $ps > .15$ ). It is important to note, for later discussion, that we did not find a significant interaction between cueing and target eccentricity,  $F(3, 45) = 1.207, p > .3$ .

*Movement time (MT).* Table 1 lists the MTs averaged across subjects for each condition. The cueing main effect for MTs was not significant,  $F(3, 45) = 1.2, p > .3$ , but the effect of SOA was,  $F(1, 15) = 19.38, p < .001$ . The MTs at the short SOA (324 ms) were faster on average than the MTs at the long SOA (345 ms), suggestive of more efficient movements at the shorter SOAs due to the

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<sup>2</sup>In the design of the current experiments, the opposite-far conditions will always have a larger cue–target distance than the within condition for the near or far targets. Therefore, the analysis of the meridian effect will only compare the invalid conditions with the same cue–target distance for a given target eccentricity, which are the within and opposite-near conditions for the near target.





**Figure 3.** RTs for the 750 ms SOA condition in Experiment 1: The RTs are shown for each cueing condition, collapsed across the near and far target eccentricities. (oppn= opposite-near; oppf = opposite-far).

longer initiation time (see RT data above). The effect of target eccentricity was also significant,  $F(1, 15) = 79.25, p < .001$ . Not surprisingly, far targets (400 ms) took longer to be reached than near targets (271 ms). None of the interactions were significant (all  $ps > .3$ ).

*Movement amplitude (MA).* The MAs for each condition are listed in Table 1. The movement amplitude measure revealed a significant effect of cueing,  $F(3, 45) = 6.73, p < .001$ , with smaller MAs for the valid conditions. Target eccentricity was also significant,  $F(1, 15) = 411.64, p < .001$ . MAs were of course smaller for the near target ( $3.56^\circ$ ) than for the far target ( $9.32^\circ$ ). The Cueing  $\times$  SOA interaction for MAs was significant,  $F(3, 45) = 3.73, p < .05$ . When the SOA was 200 ms, none of the linear contrasts was significant. In contrast, when the SOA was 750 ms, the valid condition ( $6.22^\circ$ ) was significantly shorter than the opposite conditions ( $6.63^\circ$ ),  $F(1, 15) = 11.18, p < .005$ , and the within condition ( $6.49^\circ$ ),  $F(1, 15) = 11.38, p < .004$ . The result at this 750 ms SOA are consistent with reports demonstrating a more robust and reliable IOR when the cue–target SOA is longer than 250 ms (Posner & Cohen, 1984). Because of this, and also for more direct comparisons with Experiment 2,

which only used a 750 ms SOA, our further analyses on movement amplitudes will focus on the 750 ms SOA conditions.<sup>3</sup>

The Cueing  $\times$  Target eccentricity interaction was also significant,  $F(3, 45) = 6.42, p < .001$ . Figure 4 shows, separately for each of the two eccentricities, the movement amplitudes in each cueing condition at the 750 ms SOA. When the target was presented at the 4 deg eccentricity, the valid condition had a significantly shorter MA ( $3.47^\circ$ ) than the opposite conditions ( $3.72^\circ$ ),  $F(1, 15) = 6.24, p < .02$ , but was not different from the within condition ( $3.37^\circ$ ) (Figure 4A). On the other hand, when the target was presented at the 12 deg eccentricity, the MA in the valid condition ( $8.97^\circ$ ) was significantly shorter than not only the MAs in the opposite conditions ( $9.55^\circ$ ),  $F(1, 15) = 14.84, p < .001$ , but also the MA in the within condition ( $9.60^\circ$ ),  $F(1, 15) = 10.29, p < .006$  (Figure 4B). The three-way interaction was marginally significant,  $F(3, 45) = 2.50, p = .07$ , again primarily reflecting a difference between the two SOAs, with IOR being more apparent at the longer SOA.

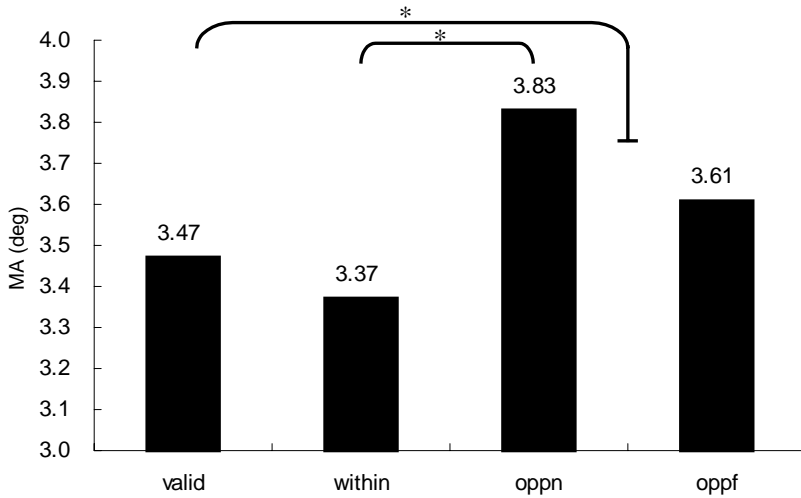
We further examined the meridian effect in MA by comparing the within and the opposite-near conditions for the near target (both have a cue–target distance of  $8^\circ$ ). At the 200 ms SOA, the MA of the within condition ( $3.39^\circ$ ) was significantly smaller than that of the opposite-near condition ( $3.75^\circ$ ),  $F(1, 15) = 5.03, p < .04$ . At the 750 ms SOA, the MA of the within condition ( $3.37^\circ$ ) was also significantly smaller than that of the opposite-near condition ( $3.83^\circ$ ),  $F(1, 15) = 45.37, p < .0001$  (Figure 4A). Hence, there was a clear meridian effect at both SOAs such that MAs toward the validly cued hemifield were smaller than those toward the near target in the opposite hemifield of the cue.

*Endpoints of movement (EOM).* The EOMs in each condition can be found in Table 1. As expected, the analyses on the EOMs were very similar to the analyses with the MAs (e.g., compare Figure 4 to Figure 5). There was a significant effect of cueing,  $F(3, 45) = 6.06, p < .001$ . Target eccentricity was significant,  $F(1, 15) = 462.50, p < .001$ . The Cueing  $\times$  Target eccentricity interaction was also significant,  $F(3, 45) = 4.74, p < .01$ .

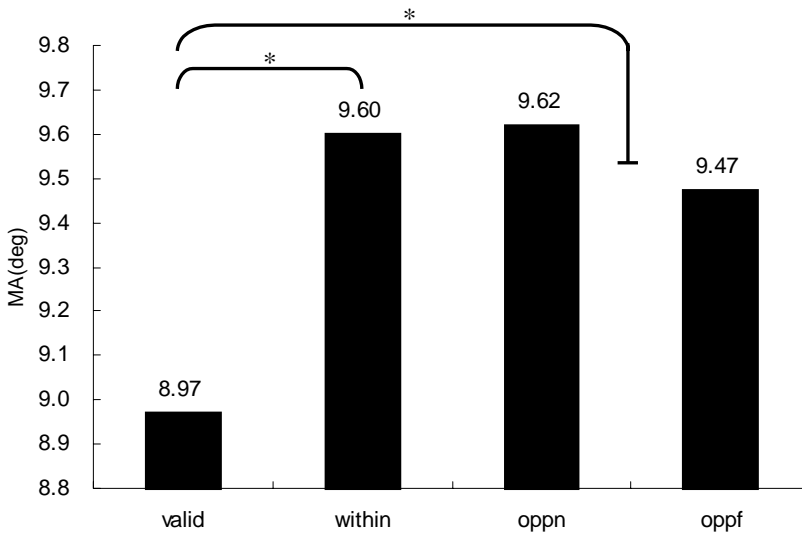
The three-way interaction was significant,  $F(3, 45) = 4.26, p < .01$ . At the 200 ms SOA, the valid condition was neither different from the opposite conditions nor from the within condition (both  $F$ s  $< 1$ ), and this was the case for both target eccentricities. At the 750 ms SOA (see Figure 5), when the target was far, the valid condition ( $10.99^\circ$ ) was less eccentric than the opposite conditions ( $11.55^\circ$ ),  $F(1, 15) = 9.81, p < .007$ , and the within condition ( $11.68^\circ$ ),  $F(1, 15) = 10.82, p < .007$ .

<sup>3</sup> The movement amplitudes at the 200 ms SOA showed a pattern of results similar to that of Experiment 2. This may have been due to the longer reaction times at this shorter SOA, which may consequently reveal perceptual processes more than motor ones (see General Discussion and Hu & Goodale, 2000).

A. Target at 4 deg

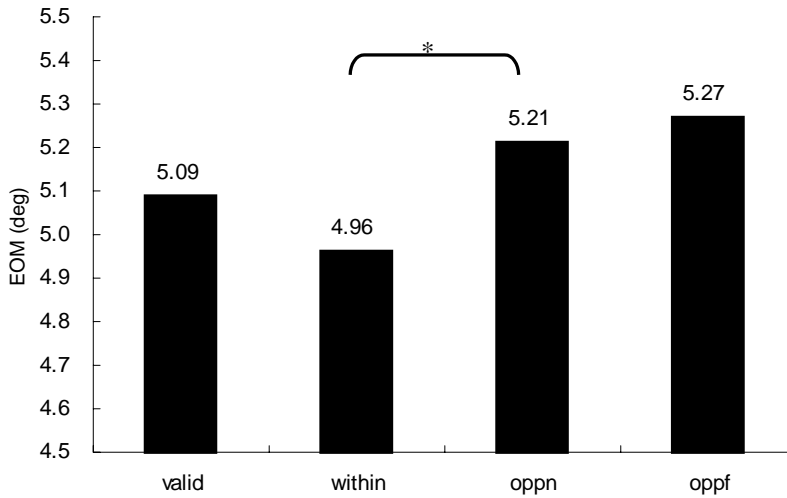


B. Target at 12 deg

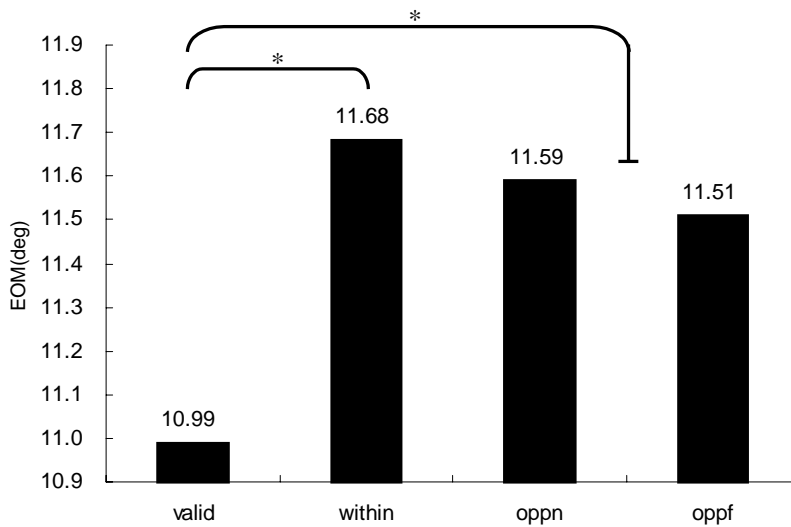


**Figure 4.** MAs for Experiment 1: The MAs are shown for each cueing condition at the 4 deg (A) and 12 deg (B) target eccentricity for the 750 ms SOA. Significant differences were bracketed and marked with an asterisk. The opposite conditions were combined when compared with the valid condition. (oppn= opposite-near; oppf = opposite-far).

A. Target at 4 deg



B. Target at 12 deg



**Figure 5.** EOMs for Experiment 1: The EOMs are shown for each cueing condition at the 4 deg (A) and 12 deg (B) target eccentricity for the 750 ms SOA. Significant differences were bracketed and marked with an asterisk. The opposite conditions were combined when compared with the valid condition. (oppn= opposite-near; oppf = opposite-far).

.005. When the target was near, the valid condition ( $5.09^\circ$ ) was not different from the opposite conditions ( $5.24^\circ$ ) or the within condition ( $4.96^\circ$ ), both  $ps > .2$ .

The meridian effect was examined by contrasting the within and the opposite-near conditions for the near target. At the 200 ms SOA, the EOM in the within condition ( $5.10^\circ$ ) was significantly smaller than that in the opposite-near condition ( $5.33^\circ$ ),  $F(1, 15) = 7.06$ ,  $p < .02$ . At the 750 ms SOA, the EOM in the within condition ( $4.96^\circ$ ) was again significantly smaller than that in the opposite-near condition ( $5.21^\circ$ ),  $F(1, 15) = 20.03$ ,  $p < .001$ .

*Error analysis.* The overall error rate was 7.70% on the average. RT and MT error rates in each condition were arcsine transformed and separately subjected to an ANOVA with the same design as that for all of the other dependent variables. The RT and MT error rates for each condition are listed in Table 1. For RT errors, the SOA was the only significant factor,  $F(1, 15) = 11.85$ ,  $p < .01$ , with a higher average error rate for the 750 ms SOA (4.52%) than for the 200 ms SOA (1.69%). For MT errors, the SOA was again the only significant factor,  $F(1, 15) = 5.72$ ,  $p < .05$ , with a higher average error rate for the long SOA (2.93%) than for the short SOA (1.60%).

## Discussion

The main results in Experiment 1 are that RTs and, of particular interest, MAs showed clear IOR effects. Specifically, reaches to targets at previously cued locations were hypometric when compared to reaches to targets appearing at any other location. In addition, there was a meridian effect in the RTs. Thus, our RT data are consistent with those in Berlucchi et al. (1989), Ro et al. (2000), Tassinari et al. (1987), and Tassinari, Biscaldi, Marzi, & Berlucchi (1994). Those studies and the current one showed prolonged onset of responses toward a validly cued *direction*, rather than only a validly cued *location*. The meridian effect in RTs alone, however, is not strong evidence for the idea that IOR directly influences the motor system. The attentional account of IOR can also accommodate the meridian effect by assuming that the attentional gradient distributes asymmetrically between the cued and uncued hemifields, and inhibition is generated only within the cued hemifield where attentional resources were allocated. A stronger case for the motor effects of IOR could be made if we can show that IOR has effects specific to the effectors used to make the response.

Another main result in the current experiment showed just such an effector-specific effect: The movement amplitudes of reaches were hypometric for both valid and within conditions for near targets, and were hypometric only for the valid conditions for far targets; an additional comparison conducted on far targets at the 750 ms SOA showed no difference between the within condition ( $9.60^\circ$ ) and the opposite conditions ( $9.55^\circ$ ),  $F(1, 15) < 1$ ,  $p > .6$ . The patterns of

MAs of reaching differed from those of saccades in Ro et al. (2000), which showed hypometric saccadic amplitudes for any target within the whole hemifield ipsilateral to the cue. To statistically confirm this difference between saccades and reaching for far targets, a two-way (task/cueing), mixed-design ANOVA was conducted on the MAs of the far targets in Ro et al. and the current experiment. The dissociation between the MAs of hand and eye movements was confirmed by a significant two-way interaction between task (eye movement/reaching) and cueing,  $F(3, 66) = 3.08, p < .05$ . The same ANOVA on the MAs of near targets did not reveal such a significant interaction ( $p = .53$ ). How can the mismatch between reaching and saccades in the patterns of spatial biases support the motor effect of IOR?

The idea that IOR has direct influence on the motor system could be supported and especially apparent when considering the nature of motor programming for saccades vs. reaching. These two motor systems have different numbers of degrees of freedom: Eye movements are two-dimensional, whereas hand movements are three-dimensional. Eye movements have three degrees of freedom whereas the joints of the arm have seven degrees of freedom (Rosenbaum, 1991). Even without the three degrees of freedom belonging to the shoulder, which was not likely to have been used by our participants, there were still four degrees of freedom in the lower arm<sup>4</sup> (Rosenbaum, 1991; Zatsiorsky, 1998) available in the reaching task. More degrees of freedom allow for flexibility in overcoming an obstacle. For instance, when an empty glass is between one's hand and a bottle of beer, instead of reaching directly for the bottle, which would mean hitting the glass, one can easily move one's hand above or around the glass and then grab the bottle. In other words, when a reaching path is blocked or inhibited, the hand-motor system is capable of resolving the difficulty by adopting another reaching path. This flexibility, based on the degrees of freedoms, is probably why IOR biased reaching differently than saccades for the far-target/near-cue within-hemifield condition; the lack of IOR on MAs for this condition likely reflects the flexibility of the reaching system in avoiding obstacles such as the near cue.

One potential confound of this experiment was the lack of eye movement monitoring and head movement restrictions, which might be the factors that may have produced the hypometric MAs in the reaching task, similar to those with saccades reported by Ro et al. (2000). For example, participants could have made eye movements toward the targets, and eye movements and eye position could have guided the hand movements. Note, however, that there were some

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<sup>4</sup>The lower arm has elbow, wrist, and radioulnar joints. The elbow has one degree of freedom (flexion–extension). The wrist has two degrees of freedom (flexion–extension and ulnar–radial deviation). The radioulnar joint has one degree of freedom (pronation–supination) (Kreighbaum & Barthels, 1996; Neumann, 2002). Some researchers assign pronation–supination to the wrist, but others assign it to the elbow (Zatsiorsky, 1998).



spatial differences, particularly in the within-hemifield conditions, between the current reaching experiment and those measured with saccades. Nonetheless, to exclude the possibility that the hypometric reaching was due to hypometric eye movements, we conducted another reaching experiment where participants' fixation was monitored and trials were discarded when they failed to remain fixation at the centre of the display.<sup>5</sup> A three-way ANOVA, with experiment (with/without eye monitoring), cueing, and target eccentricity as the factors, were conducted on the MAs of each reaching experiment. Neither the experiment by cueing interaction or the three-way interaction approached significance.<sup>6</sup> In other words, the consistent patterns of MAs in reaching experiments with and without eye monitoring ensures that the hypometric reaching was not due to hypometric eye movements.

Given the fact that eye movements did not directly drive the IOR influences on reaching, one might still question whether some form of indirect "cross-talk" between the motor maps of eye and hand movements resulted in the similar results between the current experiment and that of Ro et al. (2000). This possibility could potentially be addressed by comparing the patterns of reaching towards objects requiring similar eye movements, but different trajectories of reaching. Although such an experiment is beyond the scope of the current study,

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<sup>5</sup> Twelve participants (7 females and 5 males; mean age: 19.1 years) participated in the same reaching experiment with fixation monitored by the experimenter. An Applied Science Laboratories (Bedford, MA) Model 210 eye tracker was used to record the viewing direction of the left eye. The stimulus display that participants viewed was also shown on a TV screen via a scan converter. A vertical line representing the viewing direction was superimposed on the stimulus display. Eye movements were visible to the experimenter, who constantly observed the gaze direction on the TV. After the participant completed a trial, the experimenter determined whether that trial was discarded or not depending on whether fixation was successfully kept. Trials discarded due to eye movements were repeated later in the random sequence.

<sup>6</sup> For the remaining analyses on the MA data, the main effect of cueing was significant,  $F(3, 78) = 15.62, p < .001$ . The interaction between cueing and target eccentricity was also significant,  $F(3, 78) = 7.18, p < .001$ . These results were consistent with Experiment 1. There was a significant interaction between task and target eccentricity,  $F(1, 26) = 7.68, p < .01$ , due to the longer MAs in the new experiment ( $11^\circ$ ) compared to Experiment 1 ( $9.41^\circ$ ) when reaching toward the far target,  $F(1, 26) = 5.25, p < .05$ , but not when reaching toward the near target ( $p > .4$ ). The longer MA or EOM in the new experiment at the far target eccentricity may be because the sensor of the eye-tracking device was in between the stimulus and the eye and visible to the participant. The sensor might have served as a reference frame for the participant to estimate the distance between fixation point and targets and somehow made the reaching distance longer in the new experiment. In any case, this factor did not alter the influence of IOR on reaching. The ANOVA on the RT data from the new experiment with eye movement monitoring showed a significant effect of cueing,  $F(3, 78) = 19.17, p < .001$ , and target eccentricity,  $F(1, 26) = 18.90, p < .001$ . Linear contrasts showed that the valid (477 ms) and the within (473 ms) conditions both had longer RTs than the opposite conditions (457 ms),  $F(1, 11) = 14.02, p < .01$  and  $F(1, 11) = 13.10, p < .01$ , respectively. This is the signature pattern of IOR in RT. Importantly, none of the interactions were significant (all  $ps > .2$ ), including those involving Experiment, indicating that the RT patterns were not different between the two experiments.

the current results provide evidence for an effect on reaching that is independent of the generation eye movements.

Some other interesting effects in this experiment also warrant discussion. The current RT results did not confirm findings that IOR was determined by attentional momentum (O'Donnell & Pratt, 1996; Pratt, Spalek, & Bradshaw, 1999). O'Donnell and Pratt (1996) adopted an experimental paradigm similar to the current study. In their Experiment 1, there were also four potential cue/target locations that were aligned horizontally, and IOR was found at the near locations when the cues were presented at the far locations, but not at the far locations when the cues were presented at the near locations. O'Donnell and Pratt also found that when the cue and target were within the same hemifield, but not collinear with the direction of attentional movement (i.e., the vector from fixation to the cue), IOR could not be found. They argued that IOR was an attentional phenomenon and only occurred along the path of attentional movement. When the cue was near and the target was far, attention had never passed through the target location, hence no inhibition was found. Their explanation can be viewed as an attentional-perceptual account of IOR because it maintained that IOR occurred only where attention was directed. Contrary to their results and explanation of IOR, we showed that IOR, as measured with RTs, was observed regardless of cue/target eccentricity (and thus not necessarily along the path of attentional movement), as long as the cue and target were within the same hemifield (illustrated by the absence of a Cueing  $\times$  Target eccentricity interaction). Although the RT results in this experiment were different from those in O'Donnell and Pratt, the Cueing  $\times$  Target eccentricity interaction in the MA results was similar. This suggests that their RT results may be reflecting, perhaps in addition to attentional momentum, influences of IOR on motor, and in particular, reaching processes.

Another finding in this study was that RTs were longer to far targets than to near targets, which is consistent with other attention studies adopting simple detection and manual responses (Berlucchi et al., 1989; Tassinari et al., 1987). The opposite pattern, however, was shown in studies with saccadic tasks (Ro et al., 2000); that is, the initiation of saccades was longer to near targets than to far targets. The differential near–far RT costs for manual and saccadic responses have also been reported in Hodgson and Müller (1995) and Reuter-Lorenz and Fendrich (1992). This effect is likely due to different characteristics of the hand and eye movement systems. A systematic investigation, which controls the intensity, size, and duration of stimuli, is necessary to depict the eccentricity-latency functions of saccadic and manual responses.

By contrasting hand movement amplitudes in the current experiment with those of saccades in Ro et al. (2000), it appears that the motor theory is a relatively plausible account for the IOR effect since similar influences of IOR on RTs have been found for hand and eye movements, and the slightly different patterns of the kinematic measures in these two motor systems can be resolved

by their respective motor characteristics. To determine whether the effects of IOR on motor processes are independent from any effects on perception, in Experiment 2 we adopted the same configuration of stimuli but employed a task in which participants *indirectly* indicated (i.e., without directed reaches) the target location with a mouse cursor to specify its location. By contrasting the spatial biases in Experiment 2 with those in Experiment 1 and in Ro et al., the influences of IOR on motor and on perceptual processes might be disentangled.

## EXPERIMENT 2: IOR IN LOCALIZATION WITH THE MOUSE CURSOR

### Method

#### *Participants*

After informed consent, following the guidelines according to the declaration of Helsinki and approval by the institutional review board of Rice University, 16 Rice University students (8 males and 8 females; mean age: 24, range: 18–34) participated in this experiment, and each was paid \$4 for participation. By self-report, participants had normal or corrected-to-normal vision. One of them was left-handed but she was accustomed to using a mouse with her right hand, and did so in the experiment. One male and one female (the left-handed) participant were not included in the analysis because over 20% of their trials were discarded due to slow responses and/or highly deviated end points.

#### *Apparatus and stimuli*

The experimental settings were similar to those in Experiment 1, except that the task was changed to a localization task with a mouse, and only the 750 ms SOA was used because this was the SOA at which we measured IOR most consistently, in both temporal and spatial measures, in Experiment 1. The size of the arrow mouse cursor was  $16 \times 16$  pixels ( $0.88^\circ \times 0.88^\circ$ ) at a resolution of  $640 \times 480$ . The colour of the mouse cursor was white. In addition, participants looked at the monitor directly rather than via the image projection device, which blocked the hand and arm from view, because it was important to have the response as indirect and perceptually based as possible in order to minimize the influences from the motor system. Note that looking at the monitor directly at a spatially nonoverlapping location as the hand controlling the mouse reduces the subjective experience of directly reaching toward the target position, allowing the participants to rely more on their visual perception than their motor system.

### *Design and procedures*

The design and procedures were similar to the previous experiment with the following exceptions. The entire experiment consisted of 192 trials for each subject, with 24 trials for each combination of the Cueing (valid, within, opposite-near, opposite-far)  $\times$  Target locations (near, far). Only the 750 ms SOA was used in this experiment. Participants took a short break every 48 trials.

Throughout the experiment, subjects held their right hand on the mouse in the way they felt most comfortable. On every trial, the fixation point appeared 2500 ms before the cue appeared. The cue last for 100 ms, and then the target appeared 750 ms after the onset of the cue and was presented for 50 ms. Immediately after the target disappeared, the fixation point was replaced by the cursor at the centre of the screen and remained visible until a response. Participants had to move the cursor to where they perceived the target and then click on that location. The mouse cursor moved 13 cm on the screen for every 1 cm of mouse movement. Both speed and accuracy were emphasized. Reaction time (from the onset of the target to the click on the target location) and the endpoints of mouse pointing on the screen were recorded.

### **Results**

*Reaction time (RT).* The RTs for each condition are given in Table 2. The effect of cueing was significant,  $F(3, 39) = 4.07, p < .01$ . Figure 6 shows the mean RTs for the different cueing conditions. The linear contrast showed that responses in the valid condition (901 ms) were significantly slower than those in the opposite conditions (877 ms),  $F(1, 13) = 5.86, p < .03$ , but not different from those in the within condition (897 ms),  $F < 1, p = .69$ . The effect of target eccentricity was significant,  $F(1, 13) = 363.61, p < .001$ . Near targets were responded to faster (806 ms) than far targets (962 ms), which was consistent with the RT and MT results in Experiment 1. The two-way interaction was not significant,  $F(3, 39) = 0.55, p = .65$ . The meridian effect was analysed in a way similar to that in Experiment 1. For the near target, the comparison between the within (819 ms) and the opposite-near (805 ms) conditions was significant, but only with a one-tailed test,  $F(1, 13) = 3.68, p = .038$ .

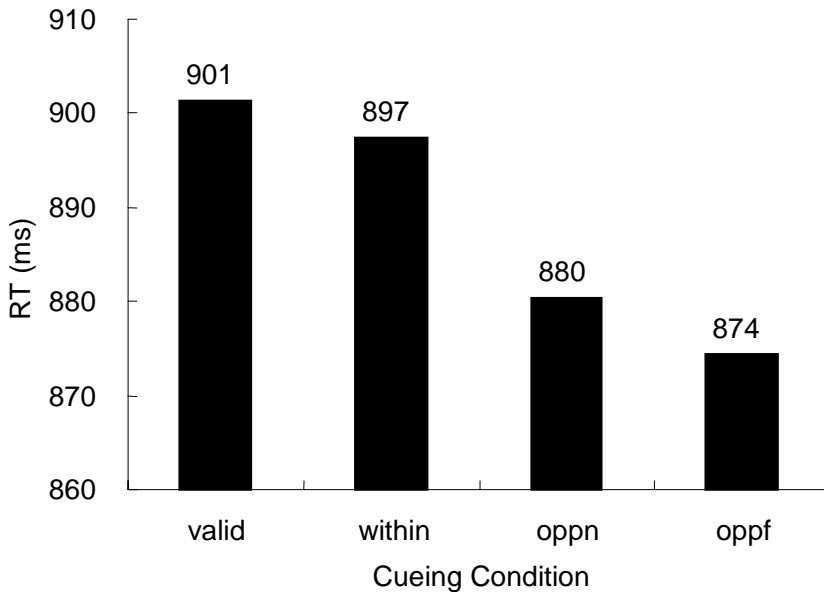
*Endpoints of movement (EOM).* The endpoints for each condition are given in Table 2. The endpoints were eccentricities measured from fixation to the location where subjects placed the cursor to indicate the target position and clicked on the mouse. Importantly, and unlike Experiment 1, the main effect of cueing was not significant,  $F(3, 39) = 0.57, p = .6$  (see Figure 7). The effect of target eccentricity was highly significant,  $F(1, 13) = 2788.83, p < .0001$ , with more eccentric endpoints for the far targets ( $11.95^\circ$ ) than for the near targets ( $3.66^\circ$ ).

The Cueing  $\times$  Target eccentricity interaction was significant,  $F(3, 39) = 12.49, p < .0001$ . As can be seen in Figure 7, the source of this significant

TABLE 2  
Means of the temporal characteristics (RT in ms), spatial characteristics (EOM in degrees of visual angle), and percentage errors for each condition in Experiment 2. Standard deviations are in parentheses

	Near target			Far target				
	Valid cue	Within cue	Oppn cue	Oppf cue	Valid cue	Within cue	Oppn cue	Oppf cue
RT	828 (110)	819 (100)	805 (98)	791 (102)	975 (119)	975 (111)	956 (108)	958 (120)
EOM	3.72 (0.39)	3.56 (0.43)	3.67 (0.39)	3.69 (0.43)	11.84 (0.80)	12.11 (0.76)	11.97 (0.82)	11.89 (0.79)
ERR <sub>rt</sub>	1.19 (1.95)	0.89 (1.77)	0.30 (1.11)	0.60 (1.51)	2.68 (5.80)	0.89 (1.77)	1.19 (2.55)	2.97 (4.14)
ERR <sub>com</sub>	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.30 (1.11)	0.60 (1.51)	0.89 (1.77)	0.60 (1.51)

Note: oppn = opposite-near; oppf = opposite-far; ERR<sub>rt</sub> = percentage of RTs longer than 1500 ms or shorter than 100 ms; ERR<sub>com</sub> = percentage of endpoints deviated more than 4 degrees from the actual target position.

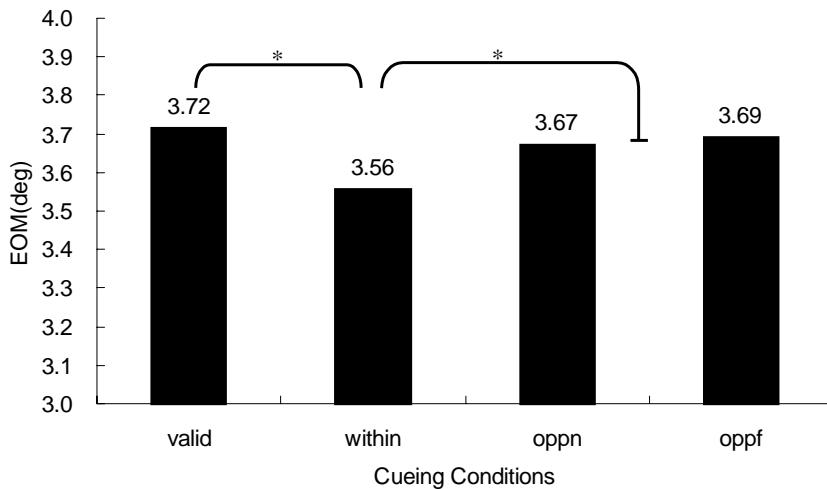


**Figure 6.** RTs for Experiment 2: RTs are shown for each cueing condition, collapsing the near and far target eccentricities. (oppn= opposite-near; oppf = opposite-far).

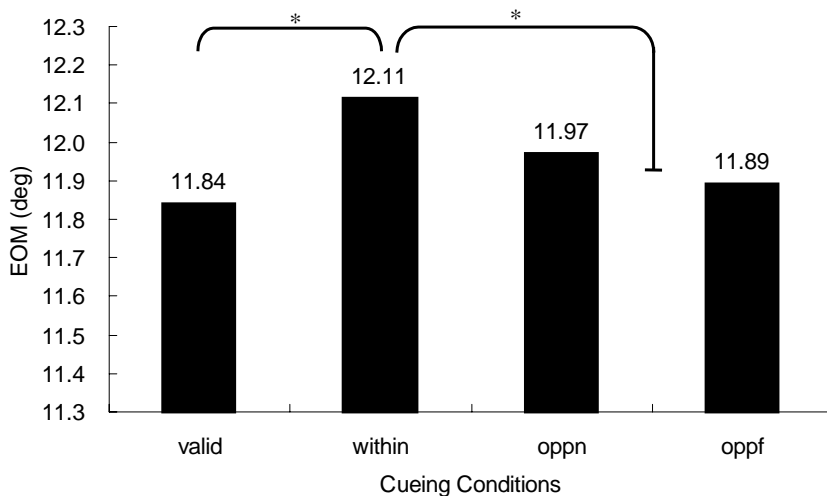
interaction came from the within conditions across the two target eccentricities. When the target was near, the within condition ( $3.56^\circ$ ) led to significantly more hypometric judgements than the valid ( $3.72^\circ$ ),  $F(1, 13) = 9.19$ ,  $p < .01$ , and the opposite conditions ( $3.68^\circ$ ),  $F(1, 13) = 8.34$ ,  $p < .01$  (Figure 7A). When the target was far, however, the within condition led to more hypermetric (i.e., less hypometric) endpoints ( $12.11^\circ$ ) than for the valid condition ( $11.84^\circ$ ),  $F(1, 13) = 22.83$ ,  $p < .001$ , and the opposite conditions ( $11.93^\circ$ ),  $F(1, 13) = 4.90$ ,  $p < .045$  (Figure 7B). Importantly and in contrast to the EOMs and MAs in Experiment 1, the EOMs in the valid conditions for both target eccentricities were not significantly different from the opposite conditions. A three-way (task/cueing/target eccentricity), mixed-design ANOVA conducted on the EOMs at 750 ms SOA from Experiment 1 and those from the current experiment showed a significant interaction between task and cueing,  $F(3, 84) = 4.82$ ,  $p < .001$ , supporting the dissociation in EOMs between the two experiments.<sup>7</sup>

<sup>7</sup> The same analysis conducted on the EOMs of the reaching task when fixation was monitored and Experiment 2 also revealed a significant interaction between task and cueing,  $F(3, 72) = 3.76$ ,  $p < .01$ . Linear contrasts showed that, in the new reaching experiment, EOMs in the valid ( $8.9^\circ$ ) and the within ( $9.0^\circ$ ) conditions were both significantly shorter than those in the opposite conditions ( $9.21^\circ$ ; both  $ps < .01$ ). In contrast, none of the cueing conditions was significantly different from each other in Experiment 2.

A. Targets at 4 deg



B. Targets at 12 deg



**Figure 7.** EOMs for Experiment 2: EOMs are shown for each cueing condition at the 4 deg (A) and 12 deg (B) target eccentricity. Significant differences were bracketed and marked with an asterisk. (oppn= opposite-near; oppf = opposite-far).

*Error analysis.* Errors, defined as RTs less than 100 ms or greater than 1500 ms or deviations greater than 4 degrees from the target were excluded from the analyses of RTs and EOMs. The average overall error rate was 1.64%.

The error rates (see Table 2) in each Cueing  $\times$  Target eccentricity condition were arcsine transformed and then subject to ANOVAs with the same design as those conducted on RTs and EOMs. For RT errors, target eccentricity was the only significant factor,  $F(1, 13) = 5.44$ ,  $p < .05$ , with more RT errors for far targets (1.93%) than for near targets (0.74%). For EOM errors, target eccentricity was also the only significant factor,  $F(1, 13) = 8.00$ ,  $p < .05$ , with higher error rates for far targets (0.60%) than for near targets (0%).

## Discussion

In Experiment 2, IOR in RTs was found, and the meridian effect was replicated. The comparison between the spatial measures in Experiment 2 (Figure 7) and Experiment 1 (Figure 5) provides important insights into the sites of IOR. There was no cueing main effect for EOM in this experiment, an outcome that differed from both the patterns of EOM and MA in Experiment 1, and the pattern of MA in Ro et al. (2000). For each target eccentricity in Experiment 2, the within condition was the odd one out that had the least eccentric EOM for the near target but the most eccentric EOM for the far target. Viewing this peculiar pattern merely as inhibition raises two difficulties. First, there was no reason for inhibition only to influence the within condition but not the valid condition for near targets. Secondly, if hypometric endpoints reflect inhibition, as Experiment 1 and the study by Ro et al. have shown, the far-target/near-cue within-hemifield condition showed the *opposite* pattern of inhibition. Therefore, we do not think IOR directly led to the spatial bias in the current task. Instead, the interaction between IOR and representational momentum might have resulted in the spatial bias observed in this experiment.

Representational momentum (RM) refers to the shifted judgement for the final position of a moving stimulus in the direction of motion or implied motion due to mental extrapolation (Freyd & Finke, 1984).<sup>8</sup> RM has been considered to be a distortion in memory “in analogy to the tendency for a physically moving object to continue along its path of motion” (Freyd & Finke, 1984, p. 126), but some recent studies have also suggested that RM has to do with perceptual processes (Kerzel, 2000; Kerzel, Jordan, & Musseler, 2001). More importantly, Hayes and Freyd (2002) recently reported that RM was magnified when attention was divided between the endpoint of a motion trajectory and another location. They had subjects perform two experiments in which observers attended to only one object (a dot), divided attention across more than one object

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<sup>8</sup>The authors are grateful to Masayoshi Nagai for constructive discussions on representational momentum.



(a dot and a square), or performed a secondary task simultaneously with the RM task. For objects moving transversely in space (always centripetally), diminished attention increased the forward shift of perceived endpoints, indicating that, under distraction of attention, the stopping point of the motion was less effectively represented.

In the current study, whenever the cue and target appeared at different locations, the cue–target sequence could be perceived as apparent motion of a dot across space. Because of IOR, attention, perhaps as a secondary consequence of altered motor processes (Rizzolatti et al., 1987), may also have been impaired within the cued hemifield. Based on Hayes and Freyd's (2002) findings, if IOR also influences attentional/perceptual processes, greater RM should be measured within the validly cued hemifield rather than within the hemifield opposite to where the cue was. This is exactly what was measured. For the near-target/far-cue within-hemifield condition, RM shifted the perceived endpoint toward the fixation dot (hypometric endpoint), and the extent of inward bias was further increased, due to the lack of attention. The near-target/near-cue valid condition should not have had any RM because no motion was implied in that condition. The near-target/near-cue opposite-hemifield and near-target/far-cue opposite-hemifield conditions had outward directions of motion, which should have led to directional biases, if any, opposite to the near-target/far-cue within-hemifield condition. However, attention on the opposite side of the cue, due to IOR, should have diminished RM (Hayes & Freyd, 2002). Conversely, the far-target within the cued hemifield likely made the perceived target location shift away from the fixation point (overshoot), and the bias was magnified by IOR-impaired attention. The other three conditions of the far target did not cause the same extent of outward bias, either due to lack of apparent motion (the valid condition) or to relatively enhanced attention (the opposite-near and opposite-far conditions).

## GENERAL DISCUSSION

The current study was designed to examine whether IOR has differential influences on motor and perceptual processes. Our findings seem to be more consistent with the motor hypothesis of IOR than the perceptual-attentional account in three respects. First, we showed that hand movements have spatial characteristics of responses very similar to those of saccades, and the minor difference between saccades and hand movements could be explained by considering the idiosyncratic characteristics within both motor systems. Second, we demonstrated that spatial biases of direct actions and those of perception as measured with an indirect response (i.e., reaching vs. spatial localization with a mouse cursor, respectively) toward the target were dissociated, with the former suggesting direct influences of IOR on hand movements and the latter explainable by the interaction between IOR, attention, and representational

momentum. Finally, the meridian effect in RTs was observed in both tasks, which indirectly supports a motor account of IOR.

One may ask, why were spatial directional biases consistent with IOR measured in the hand-reaching task of Experiment 1 and not in the mouse localization task of Experiment 2? Analogously, why did IOR and representational momentum interact in the mouse localization task but not in the hand-reaching task? We believe there are good reasons for this double dissociation. Note that the distance of the hand movement was extremely limited while moving the mouse cursor in Experiment 2 (1:13). As a result, the motoric bias in Experiment 2, if any, would have been scaled down to one-thirteenth of its size as compared to the direct reaching situation. In addition, whereas MA and EOM in Experiment 1 were likely determined before the initiation of reaching due to the lack of relevant visual input after the erasure of the target, the EOM in Experiment 2 might have remained unspecified until the mouse cursor was moved closely enough around the target location. This may have introduced a longer delay between the target presentation and the localization process in Experiment 2 than in Experiment 1. Hu and Goodale (2000) showed that by introducing delays between a visual target and a response, the responses tend to reflect perceptual processes more than motoric ones. Therefore, the influence of IOR on the motor system should have been minimal in Experiment 2 and instead the heavy reliance on visual perception may have magnified the influence of IOR on perceptual processes (e.g., representational momentum). Thus, a pattern of spatial bias dramatically different from that in the motor tasks was dominant in the mouse localization task.

One might argue, however, that the dissociated spatial biases were due to task differences rather than differential manifestation of IOR. Although we attempted to equate the tasks in all respects except for the response requirements (perception vs. action), there were still some differences. For example, and most notably, the presence of the mouse cursor in Experiment 2, which was not used in Experiment 1, might have interacted with the spatial representation of the target location and altered the spatial biases. We believe, however, that constantly viewing the mouse cursor on the screen might have made participants rely more heavily on their perception of target position in the mouse localization task of Experiment 2. As a result, a perceptual effect such as representational momentum could have been involved in determining the endpoints since the perceptual representations were likely to be more directly probed in that experiment. In the hand-reaching task of Experiment 1, however, participants had no visual feedback of where their online hand position was relative to the target throughout the trial. It is therefore conceivable that constant access to visual perceptual representations, as required in the localization with the mouse task, played a minor role in determining the MAs and EOMs in the hand-reaching task (cf. Milner & Goodale, 1995). This lack of interaction between visual perception and the hand motor system may have minimized the influence

of RM on spatial characteristics in Experiment 1 and revealed the more direct effects of IOR on action.

Recently, Briand, Larrison, and Sereno (2000), using only RTs as the dependent measure, compared the magnitude and time course of the development of IOR when manual versus saccadic responses were required. They demonstrated distinct time courses of IOR in manual and saccadic responses and suggested that facilitation and inhibition originated from separate spatiomotor maps in each motor modality and suggested that IOR must be tightly related to the motor apparatus of the response. Unlike the Briand et al. study, our results suggest that IOR could more directly influence motor processes because IOR modulates spatial characteristics of eye and hand motor systems in very similar ways, with the slight differences likely reflecting the different degrees of freedom in these motor systems. Therefore, the results from our experiment suggest that IOR may have direct influences on a supramodal spatiomotor map or that it may have secondary, but very similar influences on other spatiomotor maps as a consequence of primary alterations in the oculomotor system.

If IOR does have more direct influences on motoric behaviour than perception, as our results suggest, then the studies demonstrating perceptual influences of IOR, such as its interactions with representational momentum (Experiment 2), the modulation of  $d'$  (Handy et al., 1999), effects on temporal order judgment (Gibson & Egeth, 1994), and discrimination (Pratt, 1995; Pratt & Abrams, 1999) need to be accounted for. We propose that the impaired perception at the cued location could be the byproduct of motoric inhibition, as implied by the premotor theory of attention (Rizzolatti et al., 1987). We have shown that IOR inhibits movements toward validly cued positions and/or hemifields. Consequently, perceptual processing at the inhibited spatial region may subsequently be affected (Deubel, Schneider, & Paprotta, 1998). Since the effects of IOR were more spatially direct on reaching and saccades (hypometric biases) than on perception (indirect influences through representational momentum), it is likely that IOR acts more directly on the motor system and any perceptual biases may be a consequence of this motor effect. Furthermore, in these other studies showing perceptual modulation as a result of IOR, the sampled combinations of cue and target location were not enough to reveal hemifield inhibition, which is an additional feature of motoric inhibition. We predict that if the same paradigm as adopted in those studies were modified to have the spatial arrangement of cues and targets used in the current studies, we would obtain reduced  $d$ 's and temporal order judgement effects, not only in the valid, but also in the within-hemifield condition.

Taken together, these results and this double dissociation between the effects of IOR on perception and action suggest that IOR can have different manifestations, which are highly dependent upon the task. The way IOR modulates the spatial parameters of different types of movements (direct reaching and saccades) can be integrated into the framework suggesting that IOR has more direct

influences on motor processes than on perception. According to Milner and Goodale's conceptualization of division of labour in the human visual system (Goodale & Milner, 1992; Milner & Goodale, 1995), we think IOR may be more influential on the dorsal system. In fact, it has been shown that components of the dorsal system such as the superior colliculus (Posner et al., 1985; Sapir, Soroker, Berger, & Henik, 1999), the frontal eye fields (Ro, Farnè, & Chang, 2003), and the supramarginal gyrus (Lepsien & Pollmann, 2002) are involved in IOR manifestation. We have also demonstrated that the use of an array of different actions and detailed and direct comparisons between perception and action in more complex spatial tasks can be informative regarding the nature of IOR.

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