Inhibition of return in single and dual tasks: Examining saccadic, keypress, and pointing responses

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Two experiments are reported in which inhibition of return (IOR) was examined with single-response tasks (either manual responses alone or saccadic responses alone) and dual-response tasks (simultaneous manual and saccadic responses). The first experiment—using guided limb movements that require considerable spatial information—showed more IOR for saccades than for pointing responses. In addition, saccadic IOR was reduced with concurrent pointing movements, but manual IOR was not affected by concurrent saccades. Importantly, at the time of saccade initiation, the arm movements did not start yet, indicating that the influence on saccade IOR is due to arm-movement preparation. In the second experiment, using localization keypress responses that required only minimal spatial information, greater IOR was again found for saccadic than for manual responses, but no effect of concurrent movements was found. These findings add further support that there is a dissociation between oculomotor and skeletal-motor IOR. Moreover, the results show that the preparation manual responses tend to mediate saccadic behavior—but only when the manual responses require high levels of spatial accuracy—and that the superior colliculus is the likely neural substrate integrating IOR for eye and arm movements.

In our everyday environment, when we need to make a pointing, reaching, or grasping movement with our upper limbs, we naturally tend to make a corresponding saccadic eye movement to the desired target (Bekkering, Adam, Kingma, Huson, & Whiting, 1994; Gielen, van den Heuvel, & van Gisbergen, 1984; Neggers & Bekkering, 2000, 2001). Indeed, part of the function of the saccadic eye movement system is thought to be to provide the spatial information needed to properly plan and control guided limb movements. When such movements are made in the absence of saccades, performance invariably deteriorates (Abrams, Meyer, & Kornblum, 1990). Perhaps one of the few situations in which we make many precise manual movements in the absence of saccades is typing. Good typists rarely look down at the keyboard, yet they maintain very high levels of performance. Thus, conjoined saccadic and pointing–reaching movements may be considered typical of our everyday interactions with the environment, whereas dissociated saccade and keypress responses may be considered a learned specialty. Interestingly, a great deal of visual-attention research is based on experimental settings that resemble the latter, more limited, situation rather than the former, more general, situation. A good example of these limited situations comes from research conducted on a phenomenon known as inhibition of return.

Inhibition of return (IOR) refers to a general class of findings in which responses are more slowly initiated for targets that appear at previously cued locations than for targets that appear at uncued—or novel—locations. Although IOR has been found in over 300 studies to date, the vast majority of these studies have used variations of the original (Posner & Cohen, 1984) paradigm: remain fixated during each trial, ignore the cue because it contains no information about the upcoming target, and press a specified key as soon as the target is detected (see, e.g., Pratt, Kingstone, & Khoe, 1997; Tipper, Weaver, Jerreat, & Burak, 1994). Thus, the typical IOR study has dissociated gaze from action (which, as noted earlier, may represent a situation that is relatively unique), and the action measured is one that is arbitrary to the stimulus (which does not represent the types of guided actions we need to survive). Given this situation, the goal of the present article is to examine IOR across conjoined eye and manual movements. In order to do so, we will compare IOR across saccadic, keypress, and manual responses, both when such responses are made independently and when the manual responses are conjoined with saccades.

Although there are copious numbers of IOR studies that measured keypress responses while people maintained fixation, there is also evidence that IOR occurs for guided pointing responses. For example, Fischer, Pratt, and Neg-

gers (2003) found that IOR occurs for pointing movements to peripheral targets, but that it does not occur with central targets. Moreover, in comparing keypress and pointing responses, Briand, Larrison, and Sereno (2000) noted that at a 1,000-msec SOA, both produced IOR, although the inhibition may have been greater for the keypresses (33 msec) than for the mouse responses (19 msec; no statistics were reported for this comparison). Note that in light of the current issue, both of these studies instructed subjects to remained fixated throughout each trial.

Although only a small handful of studies have examined IOR with pointing responses, a much larger literature exists that has examined IOR with saccades. Again, the general finding is that IOR does occur with saccadic responses (Abrams & Dobkin, 1994), although here the onset of IOR occurs earlier with saccadic responses than with pointing responses (Briand et al., 2000). For example, at the 1,000-msec SOA, Briand et al. found more IOR for saccades (36 msec) than for mouse responses (22 msec), but these differences were not statistically tested. Thus, although IOR can be easily found with keypress, pointing, and saccade responses, relatively little is known about the differences in inhibition between the responses and what happens when the eyes and hands move together.

This is not to say that nothing is known about conjoined saccade and manual responses with IOR, since this has been examined in—as best we can determine—three studies. The fourth experiment of Khatoon, Briand, and Sereno (2002) compared conditions in which subjects made guided mouse or pointing movements while holding gaze at fixation with a condition in which saccades were conjointly made with the manual movements. However, Khatoon et al. were only able to obtain data for the manual movements, and there appeared to be no differences in IOR across the conditions (point alone = 3 msec, point-eye = 3 msec, mouse alone = 11 msec, mouse-eye = 7 msec; no statistics reported). The magnitudes of IOR, however, are obviously quite small, and this may have neutralized any effect of the conjoined saccades.

The other two studies that examined conjoined eye and manual movements were Li and Lin (2002) and Kingstone and Pratt (1999). In the last two experiments of their article, Li and Lin examined keypress responses made with (Experiment 6) and without (Experiment 7) conjoined saccades. They found that saccadic IOR (~11 msec) and manual-with-saccade IOR (~13 msec) were greater than manual-at-fixation IOR (~4 msec). Similarly, Kingstone and Pratt's second experiment showed more IOR for keypresses with conjoined saccades (28 msec) than without saccades (15 msec), although this difference was largely due to trials in which a distractor appeared in the opposite visual field to the target (saccade reaction times [RTs] were not measured in this experiment). Thus, there is some evidence that an accompanying saccade may increase keypress IOR.

There are, however, some possible limitations when interpreting the Khatoon et al. (2002), Li and Lin (2002), and Kingstone and Pratt (1999) data. For instance, Khatoon et al. (4 subjects) and Li and Lin (6 subjects) had relatively low power, and all three studies reported unusually small magnitudes of IOR. This was especially so in the fixation

conditions, which typically produce much larger inhibitory effects. In addition, two of the experiments (Khatoon et al., 2002; Li & Lin, 2002) were fundamentally interested in time course effect, and thus had multiple SOAs. Because of this circumstance, no statistics were conducted that directly compared IOR across the longer SOA conditions. A similar problem occurred with the Kingstone and Pratt study, since it was focused on differences between localization and identification responses and didn't directly compare keypress-alone and keypress-eye IOR in the target-without-distractor condition. Finally, only Li and Lin measured saccadic RTs, leaving the pattern of oculomotor IOR very much in doubt across these experiments. Taken together, these issues preclude making any definitive conclusions regarding IOR with eyes and hands from the existing literature.

As was noted earlier, the goal of the present study was to examine both keypress and pointing responses that are made when the eyes are fixated and when the saccades are conjoined to the manual response. In addition, saccadic responses made without accompanying manual responses were also examined. By specifically comparing pointing and saccadic responses (Experiment 1) and keypress and saccadic responses (Experiment 2), a more complete picture of IOR can emerge, and several issues regarding IOR can be addressed. The most central issue concerns the notion of the primacy of the oculomotor system in IOR. Almost 20 years ago, Rafal, Calabresi, Brennan, and Sciolto (1989) found that IOR occurred when cues—either peripheral or central—initiated the planning of saccadic eye movements. From these findings, Rafal et al. concluded that oculomotor activation is the critical factor in generating IOR. This notion is consistent with the relatively common idea that IOR represents a mechanism that aids in the efficiency of visual search by biasing attention (see, e.g., Posner, Rafal, Choate, & Vaughan, 1985) and eye movements (see, e.g., Klein & MacInnes, 1999) away from recently sampled locations. Moreover, the superior colliculus (SC)—a brain structure that is critical in the production of saccades—is also critical to the production of IOR (e.g., Sapir, Soroker, Berger, & Henik, 1999). Taken together, there is considerable evidence to suggest that IOR and the oculomotor system share a uniquely intimate relationship.

If IOR is more closely associated with the oculomotor system than with others, it is possible for us to make some predictions from the available data. First, responses that require greater collicular involvement should show larger magnitudes of IOR. Support for this prediction comes from Bekkering, Pratt, and Abrams (1996), who measured gap effects (a decrease in saccadic latency due to the removal of a fixation point, thought to occur because of disinhibition in the SC) in eye, pointing, and keypress responses. They found the largest gap effects with saccadic responses, and the smallest gap effects with keypress responses, suggesting that the magnitude of the gap effect was tied to the collicular involvement in the production of the response. Thus, we would expect more IOR with saccadic responses than with either manual response (with more for pointing than for keypress responses). Indeed, there is some evidence for this idea, since Li and Lin (2002) found more

IOR for saccades and keypress-alone responses. However, their experiment did not include pointing responses.

If IOR is especially effective in inhibiting saccades, then it may be that manual movements show greater inhibition when conjoined with saccadic responses. The notion is that manual responses may “piggyback” on the inhibition from the oculomotor system. The existing empirical data for this possibility, however, is inconclusive. Although Li and Lin (2002) and Kingstone and Pratt (1999) found more IOR for keypress–eye than for keypress-alone movements, this was not the case for the conjoined and independent pointing responses (hand and mouse) examined by Khatoon et al. (2002). This separation on response types may occur because pointing responses require considerable SC involvement (Stuphorn, Bauswein, & Hoffmann, 2000; Werner, Dannenberg, & Hoffmann, 1997), with the inhibition in the SC essentially at ceiling and leaving little room for any additional inhibition associated with the saccade responses. Presumably, keypress responses—which have much lower spatial requirements and therefore require less SC activation—are well away from any maximal level of inhibition in the SC and are thus more likely to piggyback on saccadic IOR.

It is also possible to make the reverse of the piggyback prediction, since manual responses may have a negative impact on saccadic IOR. Previous research has shown that hand movements tend to govern ocular gaze movements (Neggers & Bekkering, 2000, 2001, 2002). This assertion leads to the possibility that—assuming that manual responses in fact show less IOR—saccadic IOR is reduced by concurrent hand movements. Since none of the existing eye–manual experiments measured saccadic RTs with and without conjoined hand movements, no data currently exist that speak to the likelihood of pointing or keypress responses interfering with oculomotor IOR.

EXPERIMENT 1

The first experiment examined IOR for saccadic responses made alone, manual pointing responses made alone, and for saccadic and pointing responses made simultaneously. For nomenclature purposes, the former two conditions will be termed *single response tasks*, with the latter two conditions being termed the *dual response tasks*. As was noted earlier, because our daily lives typically involve making spatial guided-hand movements with corresponding eye movements, we chose to examine pointing responses first and then move on to keypress responses.

Method

Subjects. Fourteen subjects—mostly college students—from 19 to 30 years old, participated in the experiment. Their vision was either normal or corrected to normal. All subjects gave their informed consent and were naive about the purpose of the experiment.

Apparatus. The 2-D position of the left eye was measured with the EyeLink I system (SensoMotoric Instruments GmbH) at 250 Hz, using infrared (IR) video oculography. The IR cameras were mounted to a head support (see the following); the EyeLink helmet was not used. Hand movements were measured with the MiniBIRD system (Ascension Technology) at 100 Hz. The MiniBIRD system operates in a DC-pulsed magnetic field—generated by a transmitter—in which

the 3-D position and orientation of a small $4 \times 4 \times 8$ mm probe can be measured. The probe was attached to the index finger of each subject.

The image of a 120-Hz CRT color monitor was projected on the surface of a wooden panel that was mounted in the setup at table height and tilted 20° out of the horizontal plane by means of a semisilvered mirror. The monitor was mounted on a panel at the top of the wooden structure and faced downward—120 cm above the table surface. The angles of the panels holding the mirror and the table surface and the height of the top panel with the monitor were adjusted so that the plane through the monitors’ screen image in the mirror exactly coincided with the table surface plane (see Figure 1). By doing so, stimuli could be presented on the “table” surface where the DC-pulsed magnetic field was the strongest, and the MiniBIRD probe was measured. When the MiniBIRD transmitter is placed too close (within 100 cm) to the CRT monitor generating the stimuli, the DC-pulsed magnetic field generated by the transmitter distorts the electrode beam in the CRT monitor and deforms the image on the screen. Conversely, the vertical retrace of the cathode ray in the monitor distorts the reading of the MiniBIRD probe position when the probe is held too close to the monitor screen. Therefore, pointing directly to the monitor was not an option, and the projection method described above had to be used instead. In a darkened room, subjects had a strong impression that the stimuli were drawn directly at the table surface.

Movement recording, stimulus presentation, and real-time feedback of the measured eye- and arm-movement signals to a second monitor were all controlled on one PC by a homemade movement recording and stimulus generation software package—TrackMagic Version 2.60. This software can read the definitions for an entire experiment (stimuli and recording settings) from a customizable text

Figure 1. A schematic overview of the setup used in Experiment 1, with the MiniBIRD emitter (4) that generates the pulsed DC magnetic field, EyeLink camera (1), semisilvered mirror (3), and the monitor facing downward (2).

script. The software is written in MS Visual C++ using the OpenGL graphics library for stimulus generation.

Stimuli and Procedure. A white fixation dot (filled circle of 0.5° visual angle) on a black background was visible throughout the experiment. When subjects stably fixated this fixation cross, the trial started, and two white open square placeholders (1° , 1-pixel outline) appeared immediately, centered 8° to the left and right of the fixation cross. After 1,000 msec, the cue (a white filled-in 1° circle) appeared for 200 msec in one of the placeholders. After the circle disappeared, a fixation cue was presented (the fixation dot increased in size to 1° for 200 msec) in order to ensure that subjects reoriented attention to the fixation dot. After the fixation dot returned to its normal size, the target (filling one of the placeholders) appeared for 1,000 msec. Subjects were instructed to respond to the target ("look only," "point only," or "look and point") as quickly as possible. The cue and target locations were equally likely to occur at either placeholder. A total of 4,000 msec after the trial started, the open squares were removed, and the next trial started when subjects fixated the center again. See Figure 2 for a schematic overview of all the events.

On 20% of the trials (catch trials), a target did not appear after the fixation cue, and subjects were instructed to withhold responding on such trials. Altogether, each subject performed three blocks of 100 trials (40 cued, 40 uncued, and 20 catch trials). The order of trials within a block was pseudorandom, and the order of the blocks was counterbalanced across subjects. The three blocks consisted of single eye, single hand, and dual eye-hand conditions. In the single-eye block, subjects were instructed to only move their eyes (i.e., make a saccade) to the target, with their hands resting on their laps. In the single-hand block, subjects were instructed to move their index finger to the target while maintaining gaze at the fixation dot. In the eye-hand block, subjects were instructed to move both their eyes and their index finger to the target. If the eyes moved away from the fixation position before the target appeared on dual eye-hand or single-eye blocks—or at any time during the entire trial for hand-only blocks—a message was displayed on the screen warning the subject that he or she did not fixate, and the trial was aborted. The error trials were inserted randomly somewhere in the remaining trial sequence of that block, guaranteeing that for each block, 100 correct trials were recorded and that fixation was held at the center of the screen for the required time.

Data analysis. Onsets of saccades were analyzed in real time by the EyeLink software (using a $35^\circ/\text{sec}$ velocity threshold and $9,500^\circ/\text{sec}^2$ acceleration threshold criterion), and were stored on disk together with position samples. Offline, the RT of a saccade was calculated (using MATLAB 6.5 scripts) as the time between the onset of the target square and the onset of the first saccade thereafter. Saccades with latencies smaller than 50 msec or larger than 550 msec were considered anticipations or misses and were excluded from analyses, as were the few trials on which eyeblinks occurred during saccades.

Hand movements were analyzed using homemade MATLAB functions. The hand-movement velocity was calculated as the 3-D Euclidian distance between consecutive samples divided by the time between two samples (10 msec), and was filtered using a 4th-order Butterworth filter with a cutoff frequency of 30 Hz. The RT of a hand movement was defined as the time between target onset and the time when the velocity first exceeded a 0.2 m/sec threshold and stayed above threshold for at least 100 msec. Pointing movements with latencies smaller than 150 msec or larger than 600 msec were considered anticipations or misses and were excluded from analyses. The trials were then ordered according to condition and trial type, and the averages per condition, trial type, and subject were analyzed using a repeated measures ANOVA.

Results and Discussion

The mean saccadic and pointing RTs (see the left side of Figure 3) were analyzed with a 2 (response: saccade or pointing) $\times$ 2 (task: single or dual response) $\times$ 2 (trial type: cued or uncued) ANOVA. As expected, a main effect of re-

Figure 2. The sequence of events in a single trial. During the delay, the initial display was shown. Physical parameters: fixation dot, 0.5° ; placeholder boxes, 1.0° square; fixation-to-box distance, 8.0° ; size of fixation dot during fixation cue, 1.0° .

sponse was found [$F(1,13) = 97.2, p < .0001$], with faster RTs for saccadic (288 msec) than for pointing (405 msec) responses. Also as expected, the presence of IOR was confirmed by the main effect of trial type [$F(1,13) = 33.6$], with longer RTs for cued (355 msec) than for uncued (338 msec) trials. As predicted, the response $\times$ trial type interaction was significant [$F(1,13) = 5.7, p < .04$], with more IOR found for saccadic (23.8 msec) than for pointing (10.8 msec) responses. The task $\times$ trial type interaction was also significant [$F(1,13) = 4.8, p < .05$], with more IOR in single-response (22 msec) than in dual-response (12.5 msec) tasks. Importantly, the task $\times$ response $\times$ trial type interaction was also significant [$F(1,13) = 4.8, p < .05$], since the reduction in IOR between single-response and dual-response tasks was greater for saccades than for pointing responses (see the left side of Figure 4). No other main effects or interactions reached significance. In order to further interpret the three-way interaction, separate 2 (task) $\times$ 2 (trial type) ANOVAs were conducted on the saccadic and pointing responses. Al-

Figure 3. Mean response times (RTs) for single (eye, hand conditions) and dual (eye–hand condition) tasks from Experiment 1 (saccades and manual pointing) and Experiment 2 (saccades and manual keypress).

though the saccades showed a reduction in IOR from single-response to dual-response tasks [$F(1,13) = 5.75, p < .05$], the pointing responses did not [$F(1,13) < 1$].

Less than 8% of the trials were excluded due to either anticipatory or too slow pointing or saccades or eyeblinks (see Method), and these means are reported in Table 1.

Overall, two major findings emerged from the first experiment. As predicted, more IOR was found with saccadic responses than with pointing responses, supporting the notion that IOR may have a particular oculomotor component. In addition, the reduction of IOR occurred only for saccades in the dual task and not for pointing responses. On the one hand, it may be that simply planning and producing any two simultaneous responses (one oculomotor, one manual motor) may reduce IOR and that the saccadic system is simply more sensitive to the interference. On the other hand, the pattern of reduced IOR in the dual task that was found in the present experiment may be specific to the generation of saccades and pointing responses. In particular, both saccades and pointing movements require detailed spatial information about the target in order to program the responses. In order to further examine IOR with dual tasks, a second experiment was conducted.

EXPERIMENT 2

In Experiment 2, the pointing responses used in the prior experiment were replaced with choice (localization) keypress responses. As was noted earlier, keypress responses are far more common in the IOR literature than are pointing

responses; thus, Experiment 2 used a more typical manual response for investigating IOR with single and dual tasks. If the deficits in IOR found in Experiment 1 were due to the planning of any manual response simultaneously with a saccadic response, then a similar pattern of results (greater deficit in IOR for saccades than for keypresses in the dual condition) should be found in Experiment 2. If the previous IOR deficit occurred because guided limb movements and saccades both require detailed spatial information, then a different pattern of results should emerge with the localization keypress responses (which only require a minimum of spatial information). In this case, we would expect to find more IOR with saccades than with keypresses, but not more IOR in single than in dual tasks for either type of response.

Method

Subjects. Fifteen University of Toronto undergraduates participated in the study in exchange for course credit. All of the subjects had either normal or corrected-to-normal vision and were naive about the purpose of the study.

Apparatus, Stimuli, and Procedures. Unlike in Experiment 1, Experiment 2 used an EyeLink II eyetracker with 500-Hz cameras and no MiniBIRD limb tracking system. The stimuli and procedures were the same as those in Experiment 1, except that manual responses were now made by either left- or right-index-finger keypresses—according to the location of the target—on a game pad.

Results and Discussion

As before, the mean saccadic and keypress RTs (see right side of Figure 3) were analyzed with a 2 (response) $\times$ 2 (task) $\times$ 2 (trial type) ANOVA. Once again, a main ef-

Figure 4. The magnitudes of IOR in single- and dual-task conditions for Experiment 1 (saccades and manual pointing) and Experiment 2 (saccades and manual keypress).

fect of response was found [$F(1,15) = 73.1, p < .0001$], with RTs faster for saccadic (267 msec) than for keypress (462 msec) responses. Also as before, IOR was found—indicated by the main effect of trial type [$F(1,15) = 14.3, p < .003$]—with longer RTs for cued (375 msec) than for uncued (353 msec) trials. In addition, a main effect of task was found [$F(1,15) = 5.2, p < .04$], with shorter RTs in the single- (345 msec) than in the dual-task (383 msec) conditions. As expected, the response $\times$ trial interaction was significant [$F(1,15) = 10.3, p < .01$], with more IOR found for saccadic responses (31.9 msec) than for keypress responses (12.4 msec). The interaction of response and task also reached significance [$F(1,15) = 24.9, p < .001$], with manual responses showing a greater increase in RT in the dual-task than in the saccadic responses. Importantly, the task $\times$ trial type and task $\times$ response $\times$ trial type interactions that were seen in the previous experiment did not occur in this one [$F(1,15) < 1$] (see the right side of Figure 4). Fewer than 5% of the trials were excluded because of either anticipatory or too slow buttonpresses or saccades or eyeblinks (see Experiment 1 for error criteria and Table 1 for the mean percentage of errors).

In order to confirm that the change in saccadic IOR that was found in Experiment 1 did not occur in Experiment 2, the following analysis was performed. First, to equate across RTs from the two experiments, proportional RTs (uncued RT—cued RT) were calculated for each subject for the single- and dual-eye conditions. Then, the proportional change in IOR was calculated for each subject in the keypress and pointing groups. A one-tailed t test of these proportional changes in IOR revealed that the change found with the pointing group (.052) was signifi-

cantly larger than that found in the keypress group (.001) [$t(28) = 1.79, p < .05$]. No such change was found between the pointing (.016) and keypress (.011) groups with manual responses [$t(28) < 1$].

Replicating the first experiment, saccades produced more IOR than did manual responses. Unlike the first experiment, however, there was no decrease in IOR when saccades and keypresses were made simultaneously in comparison with when they were made independently. In other words, when the manual response requires only minimal spatial information, there is no reduction in IOR with the simultaneous planning and production of eye and keypress responses.

GENERAL DISCUSSION

Four main findings emerge from the present study. First, there was a general effect of greater IOR for saccadic responses than for pointing or keypress responses. Second, equivalent magnitudes of IOR were found for pointing and keypress responses. Third, IOR for saccadic responses was reduced when conjoined pointing responses were made, but not when conjoined keypress responses were made. Finally, the presence or absence of saccadic responses did not affect the IOR for pointing or keypress responses. Clearly, the notion of manual responses piggybacking on oculomotor IOR was not substantiated; neither manual response received an increase IOR when conjoined with saccadic responses. This result occurred despite the fact that as predicted by the notion of the primacy of IOR in the oculomotor system, saccadic responses showed greater IOR effects than did manual responses. In other words, although saccades appear to be

Table 1
Mean Percent Errors for Experiments 1 (Saccade and Pointing)
and 2 (Saccade and Keypress)

Error Type	Experiment 1				Experiment 2			
	Single Eye	Dual Eye	Single Hand	Dual Hand	Single Eye	Dual Eye	Single Key	Dual Key
RT	1.8	8.4	15.3	8.6	0.8	1.1	0.2	0
Movement	0		0		2.8		4.8	
Catch trial	0.8	0.4	0	0	3.3	4.8	4.1	4.3

Note—Reaction time (RT) errors refer to trials in which movements were initiated too early or late; movement errors refer to trials in which the wrong effector was moved (note that no such errors are possible in the dual-response tasks), and catch-trial errors refer to trials in which responses were made on catch trials (see the text for details).

especially sensitive to IOR, the inhibitory effect does not transfer from the oculomotor to the manual motor system.

In terms of the existing dual-response task IOR literature, the present results both overlap and diverge from previous findings. Part of this divergence is due to the fact that the previous findings—as was noted in the introduction—are not entirely consistent with each other. The finding of greater IOR for saccades than for manual responses is consistent with an earlier finding by Li and Lin (2002), and the finding that saccades do not bolster IOR is consistent with the finding of Khatoon et al. (2002). The latter finding is, however, at odds with those of Li and Lin, and of Kingstone and Pratt (1999). They found that IOR with keypresses was greater with concurrent saccades. There is no way to easily resolve this discrepancy, although note that the single-response conditions from the present study produced almost equal magnitudes of IOR, despite the experiments being conducted in two different countries (Experiment 1, The Netherlands; Experiment 2, Canada). Thus, in two experiments that were specifically designed to look for interactions between IOR in saccades and manual responses, no such interactions were found with either pointing or keypress responses.

Interestingly, the present results show that conjoined pointing responses—but not keypress responses—interfere with the IOR of saccadic responses. This finding is interesting, given that in the combined eye–point condition—at the time the saccade was made—no actual hand movement was initiated, since hands typically started to move well after a saccade was initiated (a finding common in the literature; Bekkering et al., 1994; Gielen et al., 1984; Neggers & Bekkering, 2000). Thus, the interference does not arise from factors associated with online control of the movement. Moreover, this interference is not due to general dual-task interference effects, since in Experiment 2, no influence of simultaneously performed keypresses on saccade IOR was observed. The mere preparation of an arm movement is apparently sufficient to alter the magnitude of IOR for saccades, despite the fact that the overall saccadic RTs are not affected.

One question remains: What might produce the pattern of results found in the present study? From a behavioral point of view, the observed influence of goal-directed hand movements on saccade IOR is in agreement with the notion that hand movements tend to govern what the eyes can do during accurate pointing. Saccade and pointing move-

ments to the same goal have RTs that are tightly correlated (Gielen et al., 1984). During pointing, ocular gaze is apparently tightly anchored to the hand movement target and cannot be deviated from it by flashing new saccade targets during pointing (Neggers & Bekkering, 2000, 2001). Even when the hands change their path in midflight, the moment at which the eyes move to the new pointing target is tightly correlated to real-time correction movements of the moving arm (Neggers & Bekkering, 2002). It is likely that sensorimotor processing for eye and hand movements is shared to some extent and largely governed by what the arms (are planning to) do. When IOR is indeed related to visual processing for action purposes, one can expect that such visuomotor processing—and hence, IOR—is altered for coordinated eye and arm movements, as compared with saccades in isolation. Evidence for this integration of arm and eye action processing can be seen from the lack of dual-task interference on the spatial pointing movements in Experiment 1 and the large dual-task interference on the nonspatial keypress responses in Experiment 2.

From a neural point of view, several findings provide support for the action-based notion outlined above. Many single-cell studies on nonhuman primates have clearly demonstrated that midbrain SC contains eye-movement neurons in an oculocentric map of space (Robinson, 1972; Sparks, 1978). These neurons directly control saccadic eye movements; afterward, electro-stimulating saccades can be observed with metrics corresponding to the stimulated location in the SC map (Glimcher & Sparks, 1993; Robinson, 1972). The SC also is the main relay station for other areas in the cortex to the brainstem oculomotor nuclei driving the eye muscles (Sparks, 2002). More recent studies reported so-called “reach neurons”—active before and around arm movements—in intermediate and deeper SC layers, where the eye-movement neurons were also found (Werner et al., 1997). This arm-movement-related signal is most likely projected to the SC from the (pre)motor cortex (Fries, 1985) and precedes arm-movement onset, after which the time course covaries with arm-movement kinematics (Werner et al., 1997). Furthermore, intermediate layer neurons appear to code the target for a reaching movement in an oculocentric reference frame (Stuphorn et al., 2000). At present, many assume that these neurons play a role in eye–hand coordination rather than directly controlling arm movements (Neggers & Bekkering, 2002; Stuphorn et al., 2000; Werner et al., 1997). Interestingly,

it appears that IOR effects are observed in the saccade map SC (Dorris, Klein, Everling, & Munoz, 2002; Sapir et al., 1999). Therefore, SC reaching neurons—whose activity also usually starts well before the actual arm movement occurs (when saccades take place in the combined movement task)—could impose their IOR pattern on the SC saccade neurons, leading to “pointing-like” IOR for saccades in a dual-task condition. Namely, SC saccade and reach neurons are located in the same layers of the SC (Werner et al., 1997) and are thus probably interconnected. As was stated above, researchers know that usually reaching movements enforce their target selection on the oculomotor system (Neggers & Bekkering, 2000, 2001). The latter effects can also be explained by SC models incorporating both types of neurons (Neggers, Raemaekers, Lampmann, Postma, & Ramsey, 2005).

Note that the neural locus of IOR phenomena is most likely not limited to only the SC (see, e.g., Dorris et al., 2002; Ro, Farnè, & Chang, 2003). One common example is that IOR can inhibit locations in space-fixed coordinates rather than retinotopic coordinates—a feature not congruent with the retinotopic maps observed in the SC. In addition, IOR interacts with working-memory (Castel, Pratt, & Craik, 2003) and letter-recognition (Bowles, Ferber, & Pratt, 2005) processes, which are cortical in nature. More cogent to the issue explored in the present study, Sumner, Nachev, Vora, Husain, and Kennard (2004) found that IOR for keypress responses elaborates visual stimuli that only stimulate short-wave retinal S cones, which do not project to the SC. From this finding, they concluded that besides subcortical, there have to be cortical mechanisms as well that can generate IOR. Interestingly, for saccades, the same S-cone stimuli that were used by Sumner et al. failed to elicit IOR, demonstrating that saccadic RTs do depend on the projections to the SC. This finding makes it likely that the IOR interference on saccades by pointing movements is located in the SC, since the SC appears to drive saccadic IOR.

Taken together, the results from the present study—in the context of previous research—shed further light on the processes and mechanisms involved in IOR. First, saccadic IOR may be considered largely a function of SC activity, and concurrent movements that also require SC activity will interfere with saccadic IOR. Manual IOR, however, may be reliant on a more distributed network of subcortical and cortical structures, allowing manual IOR to be impervious to interference by concurrent saccades. Finally, with saccadic IOR capable of generating greater inhibitory effects than manual IOR, manual IOR does not appear to piggyback on saccadic IOR. Thus, echoing earlier notions of Taylor and Klein (2000) and Abrams and Pratt (2000), there appears to be dissociation between oculomotor and skeletal-motor IOR, although the dissociation is not complete, since hands can affect eyes.

AUTHOR NOTE

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REFERENCES

- ABRAMS, R. A., & DOBKIN, R. S. (1994). Inhibition of return: Effects of attentional cuing on eye movement latencies. *Journal of Experimental Psychology: Human Perception & Performance*, **20**, 467-477.
- ABRAMS, R. A., MEYER, D. E., & KORNBLUM, S. (1990). Eye-hand coordination: Oculomotor control in rapid aimed limb movements. *Journal of Experimental Psychology: Human Perception & Performance*, **16**, 248-267.
- ABRAMS, R. A., & PRATT, J. (2000). Oculocentric coding of inhibited eye movements to recently attended locations. *Journal of Experimental Psychology: Human Perception & Performance*, **26**, 776-788.
- BEKKERING, H., ADAM, J. J., KINGMA, H., HUSON, A., & WHITING, H. T. (1994). Reaction time latencies of eye and hand movements in single- and dual-task conditions. *Experimental Brain Research*, **97**, 471-476.
- BEKKERING, H., PRATT, J., & ABRAMS, R. A. (1996). The gap effect for eye and hand movements. *Perception & Psychophysics*, **58**, 628-635.
- BOWLES, B., FERBER, S., & PRATT, J. (2005). Letter processing interferes with inhibition of return: Evidence for cortical involvement. *Cognitive Brain Research*, **25**, 1-7.
- BRIAND, K. A., LARRISON, A. L., & SERENO, A. B. (2000). Inhibition of return in manual and saccadic response systems. *Perception & Psychophysics*, **62**, 1512-1524.
- CASTEL, A. D., PRATT, J., & CRAIK, F. I. M. (2003). The role of spatial working memory in inhibition of return: Evidence from divided attention tasks. *Perception & Psychophysics*, **65**, 970-981.
- DORRIS, M. C., KLEIN, R. M., EVERLING, S., & MUNOZ, D. P. (2002). Contribution of the primate superior colliculus to inhibition of return. *Journal of Cognitive Neuroscience*, **14**, 1256-1263.
- FISCHER, M. H., PRATT, J., & NEGGERS, S. F. W. (2003). Inhibition of return and manual pointing movements. *Perception & Psychophysics*, **65**, 379-387.
- FRIES, W. (1985). Inputs from motor and premotor cortex to the superior colliculus of the macaque monkey. *Behavioural Brain Research*, **18**, 95-105.
- GIELEN, C. C. A. M., VAN DEN HEUVEL, P. J. M., & VAN GISBERGEN, J. A. M. (1984). Coordination of fast eye and arm movements in a tracking task. *Experimental Brain Research*, **56**, 154-161.
- GLIMCHER, P. W., & SPARKS, D. L. (1993). Effects of low-frequency stimulation of the superior colliculus on spontaneous and visually guided saccades. *Journal of Neurophysiology*, **69**, 953-964.
- KHATOON, S., BRIAND, K. A., & SERENO, A. B. (2002). The role of response in spatial attention: Direct versus indirect stimulus-response mappings. *Vision Research*, **42**, 2693-2708.
- KINGSTONE, A., & PRATT, J. (1999). Inhibition of return is composed of attentional and oculomotor processes. *Perception & Psychophysics*, **61**, 1046-1054.
- KLEIN, R. M., & MACINNES, W. J. (1999). Inhibition of return is a foraging facilitator in visual search. *Psychological Science*, **10**, 346-352.
- LI, C.-S. R., & LIN, S.-C. (2002). A perceptual level mechanism of the inhibition of return in oculomotor planning. *Cognitive Brain Research*, **14**, 269-276.
- NEGGERS, S. F. W., & BEKKERING, H. (2000). Ocular gaze is anchored to the target of an ongoing pointing movement. *Journal of Neurophysiology*, **83**, 639-651.
- NEGGERS, S. F. W., & BEKKERING, H. (2001). Gaze anchoring to a pointing target is present during the entire pointing movement and is driven by a non-visual signal. *Journal of Neurophysiology*, **86**, 961-970.
- NEGGERS, S. F. W., & BEKKERING, H. (2002). Coordinated control of eye and hand movements in dynamic reaching. *Human Movement Science*, **21**, 349-376.
- NEGGERS, S. F. W., RAEMAEKERS, M. A. H., LAMPMMANN, E. E. L., POSTMA, A., & RAMSEY, N. F. (2005). Cortical and subcortical contributions to saccade latency in the human brain. *European Journal of Neuroscience*, **21**, 2853-2863.
- POSNER, M. I., & COHEN, Y. (1984). Components of visual orienting. In H. Bouma & D. G. Bouwhuis (Eds.), *Attention and performance X: Control of language processes* (pp. 531-556). Hillsdale, NJ: Erlbaum.
- POSNER, M. I., RAFAL, R. D., CHOATE, L. S., & VAUGHAN, J. (1985).

- Inhibition of return: Neural basis and function. *Cognitive Neuropsychology*, **2**, 211-218.
- PRATT, J., KINGSTONE, A., & KHOE, W. (1997). Inhibition of return in location- and identity-based choice decision tasks. *Perception & Psychophysics*, **59**, 964-971.
- RAFAL, R. D., CALABRESI, P. A., BRENNAN, C. W., & SCIOLO, T. K. (1989). Saccade preparation inhibits reorienting to recently attended locations. *Journal of Experimental Psychology: Human Perception & Performance*, **15**, 673-685.
- RO, T., FARNÈ, A., & CHANG, E. (2003). Inhibition of return and the human frontal eye fields. *Experimental Brain Research*, **150**, 290-296.
- ROBINSON, D. A. (1972). Eye movements evoked by collicular stimulation in the alert monkey. *Vision Research*, **12**, 1795-1808.
- SAPIR, A., SOROKER, N., BERGER, A., & HENIK, A. (1999). Inhibition of return in spatial attention: Direct evidence for collicular generation. *Nature Neuroscience*, **2**, 1053-1054.
- SPARKS, D. L. (1978). Functional properties of neurons in the monkey superior colliculus: Coupling of neuronal activity and saccade onset. *Brain Research*, **156**, 1-16.
- SPARKS, D. L. (2002). The brainstem control of saccadic eye movements. *Nature Reviews Neuroscience*, **3**, 952-964.
- STUPHORN, V., BAUSWEIN, E., & HOFFMANN, K.-P. (2000). Neurons in the primate superior colliculus coding for arm movements in gaze-related coordinates. *Journal of Neurophysiology*, **83**, 1283-1299.
- SUMNER, P., NACHEV, P., VORA, N., HUSAIN, M., & KENNARD, C. (2004). Distinct cortical and collicular mechanisms of inhibition of return revealed with S cone stimuli. *Current Biology*, **14**, 2259-2263.
- TAYLOR, T. L., & KLEIN, R. M. (2000). Visual and motor effects in inhibition of return. *Journal of Experimental Psychology: Human Perception & Performance*, **26**, 1639-1656.
- TIPPER, S. P., WEAVER, B., JERRETT, L. M., & BURAK, A. L. (1994). Object-based and environment-based inhibition of return of visual attention. *Journal of Experimental Psychology: Human Perception & Performance*, **20**, 478-499.
- WERNER, W., DANNENBERG, S., & HOFFMANN, K.-P. (1997). Arm-movement-related neurons in the primate superior colliculus and underlying reticular formation: Comparison of neuronal activity with EMGs of muscles of the shoulder, arm and trunk during reaching. *Experimental Brain Research*, **115**, 191-205.

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