Oculomotor inhibition of return: How soon is it “recoded” into spatiotopic coordinates?

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Published online: 26 May 2012
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Abstract When, in relation to the execution of an eye movement, does the recoding of visual information from retinotopic to spatiotopic coordinates happen? Two laboratories seeking to answer this question using oculomotor inhibition of return (IOR) have generated different answers: Mathôt and Theeuwes (Psychological Science 21:1793–1798, 2010) found evidence for the initial coding of IOR to be retinotopic, while Pertzov, Zohary, and Avidan (Journal of Neuroscience 30:8882–8887, 2010) found evidence for spatiotopic IOR at even shorter postsaccadic intervals than were tested by Mathôt and Theeuwes (Psychological Science 21:1793–1798, 2010). To resolve this discrepancy, we conducted two experiments that combined the methods of the previous two studies while testing as early as possible. We found early spatiotopic IOR in both experiments, suggesting that visual events, including prior fixations, are typically coded into an abstract, allocentric representation of space either before or during eye movements. This type of coding enables IOR to encourage orienting toward novelty and, consequently, to perform the role of a foraging facilitator.

Keywords Spatial vision · Eye movements · Visual attention · Inhibition of return

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Efficient sampling of the visual world, when achieved by changes in gaze direction, is determined by a multitude of factors. In visual search, for example, task demands (cf. Dodd, Van der Stigchel, & Hollingworth, 2009; Smith & Henderson, 2009), bottom-up factors that concern the natural salience of objects (see Wolfe & Horowitz, 2004, for a review), and importantly, a “memory” of previously sampled locations (cf. Peterson, Beck, & Vomela, 2007) are all at play. One mechanism proposed to afford this memory function is known as *inhibition of return* (IOR; Itti & Koch, 2001; Klein, 1988; Klein & MacInnes, 1999; Posner & Cohen, 1984). IOR, in broad strokes, refers to the robust phenomenon of increased saccadic or manual response times to targets in previously inspected locations, relative to those in previously unattended, and distance-matched, locations.

IOR is traditionally explored in a cueing paradigm in which a peripheral onset target is preceded by an uninformative peripheral cue. The peripheral cue is believed to automatically capture attention when, at short cue–target onset asynchronies (CTOAs), processing of targets is faster when they are presented at cued rather than at uncued locations (facilitation effect). At longer CTOAs, processing of targets at the cued location is hindered (IOR effect). Both mechanisms are ecologically important. The facilitation mechanism prioritizes the processing of salient events in the environment, while IOR encourages orienting toward novel locations (Posner & Cohen, 1984; Posner, Rafal, Choate, & Vaughan, 1985), and thus facilitates foraging behaviors (Klein, 1988; Klein & MacInnes, 1999).

With each successive eye movement, objects within the visual field are represented in new retinal coordinates. To function effectively as a foraging facilitator (Klein & Dukewich, 2006), IOR must be coded in spatiotopic rather than merely in retinotopic coordinates. Note that in using the term “spatiotopic,” we are referring to a nonretinotopic, environmental reference frame. This is exactly what Posner

and Cohen (1984) found in their seminal report on IOR (see also Maylor & Hockey, 1985). However, the spatiotopic reference frame was put in question by Golomb, Chun, and Mazer (2008), who proposed that the “visual system’s native or low-level representation of endogenously maintained spatial attention is retinotopic, and remapping of attention to spatiotopic coordinates occurs slowly and only when behaviorally necessary” (p. 10654). In response to this claim, two recent studies (Mathôt & Theeuwes, 2010; Pertzov, Zohary, & Avidan, 2010) have explored the time course of the retinotopic and spatiotopic coding of IOR with a task similar to that used by Maylor and Hockey.

The sequence of events in a typical trial in both studies (i.e., Mathôt & Theeuwes, 2010; Pertzov et al., 2010) was similar: IOR was generated by presenting an uninformative, to-be-ignored peripheral onset signal (*cue*). A saccade was executed in response to a peripheral onset signal (*shift stimulus*), which later allowed for saccade response time (SRT) measurements in two reference frames (i.e., spatiotopic and retinotopic). Following this intervening saccadic eye movement, at varying intervals after termination of the saccade, a final saccade signal (which we will refer to as the *target*) was delivered. The target was presented at the same screen location as the cue (spatiotopic), at the same location on the retina of the participant (retinotopic), or at one of two control locations—respectively, to the spatiotopic and retinotopic targets. Thus, the targets allowed the researchers to evaluate whether any cueing effects were present and to determine the reference frames within which those effects existed. Despite these similarities, the two investigations reported dramatically different patterns of results for the nature of the representation immediately following the first saccade (see Fig. 1, where the empirical discrepancy is highlighted by the rectangle): Mathôt and Theeuwes (2010) reported initial retinotopic coding of IOR, whereas Pertzov et al. (2010) reported initial spatiotopic coding. As suggested by Mathôt and Theeuwes (2010), “This apparent discrepancy warrants further scrutiny” (p. 1796). Our goal in the present study is to apply such scrutiny.

Important methodological features of Mathôt and Theeuwes (2010) and Pertzov et al. (2010)

Following the methods of Golomb et al. (2008), while improving upon them (notably by having two separate target locations to provide baselines against which to measure retinotopic and spatiotopic IOR), Mathôt and Theeuwes (2010) used a *quasirandom* arrangement of shift stimuli and cues. In contrast, Pertzov et al. (2010), while also using separate baselines for estimating the two forms of IOR, used a much more *rigid* arrangement, akin to that used by Maylor and Hockey (1985). This difference is illustrated in Fig. 2a–d. At the

Fig. 1 The time courses of retinotopic (open symbols) and spatiotopic (filled symbols) inhibition of return (IOR; y-axis) from Pertzov et al. (2010; plotted as squares) and Mathôt and Theeuwes (2010; plotted as triangles). The x-axis refers to the time between the achievement of fixating the shift stimulus and the onset of the target stimulus. The rectangle highlights the apparent discrepancy between Pertzov et al. (2010) and Mathôt and Theeuwes (2010). The data from Pertzov et al. (2010) are restricted to their “opposite-sides” condition; see note 1 for an explanation

beginning of a trial in Pertzov et al. (2010), participants fixated the center of the screen, and the cues and targets could be presented at four or eight fixed locations, respectively, centered around fixation (Fig. 2a). There were only two possible shift stimuli (and, consequently, first saccades), which were 7 deg to the left or the right of fixation. In contrast, in Mathôt and Theeuwes (2010), the shift stimuli (and first saccades), which were always 6 deg from fixation, were in randomly selected directions (with the restriction that neither they nor the four possible targets that might be delivered could fall off the screen; see Fig. 2d). The possible cue and target locations (always of 4.2 deg eccentricity) were centered around fixation. The major procedural difference between these studies lay in their use of fixed versus random locations for the cues, shift stimuli, and targets. Since Pertzov, Avidan, and Zohary (2011) found early spatiotopic IOR using fixed displays,¹ while

¹ At the beginning of each trial in Pertzov et al. (2010), the upcoming target might be presented at any of eight possible fixed locations, centered on the initial fixation point (Fig. 2a). After the cue and the shift stimulus, there were only four possible target locations. Importantly, the combination of the cue and shift stimulus locations might shift (when these were in the *same direction*) or might not shift (when these were in *opposite directions*) the center of gravity of locations on the screen that might contain the target (compare Fig. 2b and 2c with 2a). Because, particularly in the context of a study with fixed locations, the shift in attention that is warranted on the *same-direction* trials might have somehow interfered with the natural coding of IOR, in Fig. 1 we have only illustrated the opposite-direction condition from Pertzov et al. (2010). Even when all of the data from the shortest interval used by Pertzov et al. (2010) are combined, there was substantial spatiotopic IOR that was about 9 ms greater than the retinotopic IOR observed at this time period. This is almost precisely the opposite pattern from the one reported by Mathôt and Theeuwes (2010).

Fig. 2 (a)–(d) Methods that have been used to explore the time course of retinotopic versus spatiotopic oculomotor IOR: (a)–(c) in Pertzov et al. (2010), and (d) in Mathôt and Theeuwes (2010). In these panels, F indicates the initial fixation on a trial, S the shift stimulus locations, and C the cued locations. Possible target locations are indicated by empty circles or circles with Cs. The circles are shown only for illustrative purposes; they were not present on the screen. (a) The possible locations of fixation, cue, and shift stimuli were fixed in Pertzov et al. (2010). Fixation always started at the center of the screen, and at that time all of the locations that might be stimulated (either by cues, shift stimuli, or targets) were similarly centered at the middle of the screen.

(b) and (c) 700 ms following the onset of a cue at one of the four possible cue locations, a shift stimulus was presented at one of two possible locations. (d) In Mathôt and Theeuwes (2010), there were no fixed locations for the different types of stimuli, each of which, more or less, could appear anywhere on the screen. Illustrated here are the possible target locations, given the initial fixation stimulus, shift stimulus, and cue. The target and cue locations were selected randomly with the restriction that neither could be off the screen. (e) Cue and shift stimuli used in Mathôt and Theeuwes (2010), Pertzov et al. (2010), and our Experiments 1 and 2

Mathôt and Theeuwes (2010) did not find significant spatiotopic IOR using random locations, it is possible that spatiotopic coding may be faster, more likely, and/or more powerful *when the locations where task-relevant events occur are distinct*, as they would be when these events occur at fixed locations. This possibility will be referred to as the *location-salience hypothesis*.

A second procedural difference between the two experiments concerned the degrees to which the cue and shift stimulus were distinct. This distinctiveness may have practical and conceptual significance. The practical significance concerns task difficulty: Participants reported extreme difficulty following the instructions to ignore the cue, saccade to the shift stimulus, and then saccade to the target when using the paradigm sent to us by Mathôt and Theeuwes (2010). We hypothesized that the critical factor responsible for this difficulty was the high similarity between the cue and shift stimuli (see Fig. 2e), both being unfilled circles in the same shade of grey. This similarity alone might not have been a problem if the cue and shift stimuli had been separated by a sufficient interval, or were always presented at different locations (as in Pertzov et al., 2010). However, in Mathôt and Theeuwes (2010), the cue and shift stimuli were close together temporally (separated by only 150 ms) and over the course of a block of trials, the cues and shift stimuli alike

could appear, more or less, anywhere on the screen. None of these factors were operating in Pertzov et al. (2010). First, as is illustrated in Fig. 2e, the cue and shift stimuli were different shapes and were differently filled. Second, the cue and shift stimuli were separated by 700 ms. Finally, for the entire experiment, the shift stimulus locations and the locations where cues and targets could appear were tightly separated. It is possible that the highly demanding stimulus selection and/or response competition that characterized the Mathôt and Theeuwes (2010) methodology may have delayed the dynamic remapping of IOR from retinotopic into spatiotopic coordinates. The absence of such competition between the cue and shift stimuli in Pertzov et al. (2010), on the other hand, may have allowed for rapid presaccadic transformation from retinotopic into spatiotopic coordinates. This possibility will be referred to as the *feature-salience hypothesis*.

Other differences between the two studies are apparent with regard to the timing of the events of a trial. In Pertzov et al. (2010), the interval between the onsets of the cue and shift stimuli was 700 ms, considerably longer than the 150 ms used by Mathôt and Theeuwes (2010). In Mathôt and Theeuwes (2010), the timing of the target was fixed in relation to the cue (with CTOAs of 500, 800, 1,100, and 1,400 ms), whereas in Pertzov et al. (2010) the delivery of

the target was gaze contingent and occurred 10, 250, or 600 ms after the participants had fixated the shift stimulus. Because of these methodological differences, the CTOAs were variable in Pertzov et al. (2010) (approximately 960, 1,200, and 1,550 ms), while the end saccade–target intervals were variable in Mathôt and Theeuwes (2010) (approximately 70, 350, 640, and 920 ms). Despite these differences, there was good agreement between the studies about spatiotopic coding at long intervals, but they disagreed dramatically about how early spatiotopic coding of IOR could be observed.

The experiments

The key question addressed here was whether, immediately after an eye movement, IOR generated by a cue and measured by a saccade would be represented in spatiotopic coordinates. Even if the fixed procedure used by Pertzov et al. (2010) were not untoward, we prefer the quasirandom procedure of Mathôt and Theeuwes (2010) and Golomb et al. (2008). One reason for this is related to the functional significance of IOR as a novelty-seeking mechanism (Posner & Cohen, 1984) and foraging facilitator (Klein, 1988). If these functions are to operate in the real world, IOR would need to be present, and coded spatiotopically, in a richer and more random world than the one explored by Pertzov et al. (2010). Consequently, we decided to use the quasirandom procedure of Mathôt and Theeuwes (2010). Because our question was about the relative magnitudes of retinotopic versus spatiotopic IOR immediately after an eye movement, we chose to use the gaze-contingent delivery of the target from Pertzov et al. (2010). Finally, while keeping the timing of the cue and shift stimuli the same as in Mathôt and Theeuwes (2010), we also manipulated the degree to which these two stimuli (the cue and the shift stimulus) could be distinguished (see Fig. 2e). Whereas in both of our experiments the cue and shift stimuli differed in terms of size and fill, in Experiment 1 the cue and the shift stimulus could be easily distinguished on the basis of a difference in brightness, whereas in Experiment 2 this salient difference was eliminated.

The locational-salience and featural-salience hypotheses described above were simultaneously tested by our combination of Mathôt and Theeuwes's (2010) quasirandom presentation of all stimuli with our manipulation of the discriminability of the cue from the shift stimulus. If early spatiotopic coding is in part dependent on an internal representation of plausible shift stimulus locations, as would be encouraged by stability in the locations of the cues, shift stimuli, and targets (the locational-salience hypothesis), then, because we were using a quasirandom selection of the cue, shift stimulus, and target locations (cf. Pertzov et

al., 2010), we should find that retinotopic IOR was greater than spatiotopic IOR (as reported by Mathôt & Theeuwes, 2010). If, however, early spatiotopic coding is dependent on the ease with which the target for a saccade (in this case, the shift stimulus) can be selected (the featural-salience hypothesis), then spatiotopic IOR should be greater than retinotopic IOR when selection is easy (as in Pertzov et al., 2010), and this pattern should be reduced, if not reversed, when selection is difficult (as in Mathôt & Theeuwes, 2010).

Experiment 1

Method

Participants A group of 12 naive participants (11 female, 1 male) were tested in Experiment 1. The participants were university students who volunteered to participate for course credit. They all reported normal or corrected-to-normal visual acuity, and their average age was 21 years.

Stimuli and procedure The stimuli and procedure used in Experiment 1 were similar to those of Mathôt and Theeuwes (2010). All of the stimuli were presented on a 19-in. ViewSonic Optiquest Q95-3 CRT monitor (refresh rate = 100 Hz) connected to an Intel Core Duo processor, at a viewing distance of 22.5 in. Eye movement responses were recorded by means of an Eyelink II head-mounted eyetracking system that was connected to a host computer operating on a Pentium 4 processor. The velocity threshold used to determine whether a saccadic eye movement was made was set to 35 deg/s, and saccadic response times (SRTs) were computed by subtracting the time at which the eye movement exceeded the velocity threshold from the time at which the imperative stimulus appeared onscreen. To ensure an accurate recording of the gaze coordinates, a nine-point calibration procedure was administered to the observers before the experiment. To further ensure an accurate reading of gaze position, the successful completion of a drift correction phase was required at the beginning of each trial.

After the drift correction, a filled gray fixation disk ($d = 0.5$ deg) appeared onscreen. The participants were required to fixate this gray dot until it moved to a new location. A total of 750 ms after the appearance of the fixation disk, a peripheral onset cue was presented at a location 4.2 deg of visual angle from the fixation disk. This onset cue was a white unfilled circle (diameter [d] = 1.0 deg) presented for 50 ms. Then, 150 ms after the appearance of the cue, the fixation disk (the shift stimulus) stepped to a location that was 6 deg from the original location and 4.2 deg from the cued location. If a participant's eyes deviated more than 1 deg from the fixation disk before it moved, the trial was aborted. The termination of a successful eye movement to

the shift stimulus was used to trigger the presentation of the target, which was a bright green disk ($d = 0.5$ deg). According to our eye-monitoring equipment and software, the average interval between termination of the shift-stimulus-directed saccade and the appearance of the target was 42 ms. The target called for a saccadic response within 750 ms, and failure to respond to the target within this period led to the trial being aborted. As is illustrated in Fig. 2d, the target was presented with equal probability at one of four randomly selected locations: the cued location (cued spatiotopic location), a location 6 deg from the cued location and 4.2 deg from the shift stimulus location (uncued spatiotopic location), another location 6 deg from the cued location and 4.2 deg from the shift stimulus location (cued retinotopic location), and a location 6 deg from the uncued spatiotopic location and 4.2 deg from the shift stimulus location (uncued retinotopic location). An algorithm was implemented to guarantee that none of these four possible target locations would fall off the screen. All aborted trials were recycled and presented to the participant in a random order.

Results and discussion

A total of 8.4 % of the trials were excluded because the final saccade deviated by more than 2.0 deg from the target's location. Some 3.6 % of the trials were excluded because the saccade to the shift stimulus deviated by more than 2.0 deg from the shift stimulus's location. Finally, less than 1.0 % of the trials were excluded because of extremely fast ($SRT < 100$ ms) or slow ($SRT > 500$ ms) saccadic response times to the target. All of the SRTs and exclusions for each level of the factors Cueing and Coordinates can be found in Table 1.

SRTs to the targets (see Table 1) were subjected to an analysis of variance (ANOVA) that revealed significant main effects of Coordinates [$F(1, 11) = 88.55, p < .001$]

Table 1 Saccadic response times (SRTs) and numbers of trial exclusions for each level of the factors Cueing (cued or uncued) and Coordinates (retinotopic or spatiotopic)

	Retinotopic			Spatiotopic		
	Cued	Uncued	IOR	Cued	Uncued	IOR
SRT (ms)						
Experiment 1	212.2	192.5	19.7	263.3	228.7	34.6
Experiment 2	222.7	205.3	17.4	256.5	234.2	22.3
Trial Excluded (%)						
Experiment 1	15.5	14.2	–	11.0	8.8	–
Experiment 2	17.7	18.1	–	9.4	13.3	–

IOR is the difference score between cued and uncued locations.

and Cueing [$F(1, 11) = 56.31, p < .001$]. These main effects reflected that, overall, IOR was significant and SRTs testing retinotopic coding were faster than SRTs testing spatiotopic coding. The two-way interaction between coordinates and cuing was significant [$F(1, 11) = 6.35, p < .05$], reflecting the finding that spatiotopic IOR was greater than retinotopic IOR. This pattern demonstrates that spatiotopic IOR can be encoded before, during, or very shortly after a saccade. This pattern contrasts with that reported by Mathôt and Theeuwes (2010; retinotopic IOR > spatiotopic IOR). Given that cue–target similarity is the most noteworthy methodological difference between the present investigation and Mathôt and Theeuwes (2010), this finding is consistent with the featural-saliency hypothesis.

Experiment 2

Method

Participants A group of 12 naive participants (11 female, 1 male), who were not tested in Experiment 1, were tested in Experiment 2. Their average age was 21 years. The participants were selected from the university population and performed for course credit. All reported normal or corrected-to-normal visual acuity.

Stimuli and procedure Experiment 2 was identical to Experiment 1, with one exception: a gray (as opposed to a white) unfilled circle ($d = 1.0$ deg) served as the onset cue (see Fig. 2e). More explicitly, as compared to Experiment 1, the cue onset and the switch stimulus were more similar on the luminance dimension.

Results and discussion

A total of 10.6 % of the trials were excluded because the final saccade deviated by more than 2.0 deg from the target's location. Some 3.3 % of the trials were excluded because the saccade to the shift stimulus deviated by more than 2.0 deg from the shift stimulus's location. Finally, less than 1.0 % of the trials were excluded because of extremely fast ($SRT < 100$ ms) or slow ($SRT > 500$ ms) saccades to the target. All SRTs and exclusions for each level of the factors Cueing and Coordinates can be found in Table 1.

SRTs to the targets (see Table 1) were subjected to an ANOVA that revealed significant main effects of Coordinates [$F(1, 11) = 25.03, p < .001$] and Cueing [$F(1, 11) = 23.16, p < .001$]. These main effects reflect that, overall, IOR was significant and that SRTs testing retinotopic coding were faster than SRTs testing spatiotopic coding. In contrast to the results of Experiment 1, the two-way interaction did not approach

significance [$F(1, 11) = 1.102, p > .3$]. This pattern (retinotopic equal to spatiotopic IOR) does not replicate the pattern reported by Mathôt and Theeuwes (2010; retinotopic IOR > spatiotopic IOR; see the General Discussion for an explanation), nor does it replicate the pattern reported in Experiment 1 (spatiotopic IOR > retinotopic IOR). Taken together, however, the present and extant data are consistent with the featural-saliency hypothesis (see the section on Spatiotopic Coding and the Featural Saliency Hypothesis below), but not against the locational-saliency hypothesis (see the section on Spatiotopic Coding and the Locational Saliency Hypothesis below).

General discussion

Three main findings emerged from our experiments. First and foremost, cue-generated IOR appears to be coded spatiotopically almost immediately after a postcue eye movement. This implies that visual events are coded into spatiotopic (and possibly allocentric) coordinates either before or during eye movements (see also Pertzov et al., 2011; Tatler & Land, 2011). Second, at this point in time, spatiotopic IOR can be larger than retinotopic IOR (Exp. 1). Third, we observed a consistent benefit for second saccades that moved the eyes forward (in the retinotopic direction), as opposed to backward (in the spatiotopic direction).

The discrepancy between Mathôt and Theeuwes (2010) and the present experiments

Despite our close replication of most of the methods of Mathôt and Theeuwes (2010), we never observed their pattern of results that shortly after a saccade spatiotopic IOR was numerically smaller than retinotopic IOR and was not statistically significant. To help resolve this discrepancy, we consulted with Mathôt, and eventually requested and received trial-by-trial data from the Mathôt and Theeuwes (2010) experiment. Because we are more concerned about the relative magnitudes of spatiotopic and retinotopic IOR immediately following the saccade to the shift stimulus, we initially applied the same data exclusion criteria of Mathôt and Theeuwes (2010) and performed an ANOVA on the SRTs of their shortest CTOA. This analysis revealed significant main effects of Coordinates [$F(1, 13) = 7.83, p < .05$] and Cueing [$F(1, 13) = 5.02, p < .05$]. Consistent with, but not demonstrating, stronger retinotopic IOR, a marginally significant interaction between Cueing and Coordinates was also observed [$F(1, 13) = 3.73, p = .08$]. When we examined the distribution of their participants' SRTs to targets, we recognized that their lower bound of exclusion (50 ms, as reported at the beginning of their Results section, p. 1795) was far too low (see Fig. A1 in the Appx.), so we reanalyzed their data using the same lower bound as in the analysis of our data (100 ms), and as seemed appropriate for

their data set given the distribution. For their shortest CTOA, the main effect of Coordinates was significant [$F(1, 13) = 18.1, p < .001$], and the main effect of Cueing was marginally significant [$F(1, 13) = 3.89, p = .07$]. However, the marginally significant interaction between Coordinates and Cueing went away [$F(1, 13) = 0.02, n.s.$], suggesting that retinotopic and spatiotopic IOR were equivalent (both were about 10 ms). With this result in hand, the original discrepancy that motivated our experiments was considerably diminished. As reported by Pertzov et al. (2010), cue-generated spatiotopic and retinotopic IOR are generally both present immediately after a saccade.

To the extent to which one believes that the pattern of data that includes extremely/impossibly fast SRTs might be theoretically meaningful, one might consider reanalyzing the data in the present investigation with the same SRT cutoffs used by Mathôt and Theeuwes (2010). It is important, however, to recognize that fast (< 100 ms) SRTs were rare in our experiments. It perhaps then comes as little surprise that including these inordinately fast SRTs in our analyses did not change the pattern of results. Why/how Mathôt and Theeuwes's (2010) participants made so many extremely, if not impossibly, fast saccades to the targets (5.56 %) remains a puzzle to us. In any event, we believe that those SRTs should be excluded from analyses because they are unlikely to have been responses to the target.

Spatiotopic coding and the featural-saliency hypothesis

According to the featural-saliency hypothesis, spatiotopic IOR may depend on cue-shift stimulus discriminability. To explore the degree to which this factor might be important, we considered on how many dimensions the cue and shift stimuli differed in each of the key studies that have examined retinotopic versus spatiotopic coding of IOR using saccadic responses (see Table 2). As can be seen in Fig. 3, retinotopic IOR immediately after a saccade is relatively unaffected by the difficulty of selecting the saccade metrics, while spatiotopic IOR immediately after a saccade is substantially affected. This interesting difference is certainly worthy of further investigation. For example, new experiments would be required to determine whether the difference is related to the nature of the spatial attention that the cue is receiving when selecting against the cue is difficult, or whether it is due to the competition for the limited processing resources that may be required by both this selection process and the computations assumed to be required for spatiotopic remapping.

Spatiotopic coding and the locational-saliency hypothesis

It is not possible to definitively rule out the "locational-saliency hypothesis," despite our finding evidence that cue-target

Table 2 Cue-shift stimulus discriminability on the features of brightness, size, fill, shape, and relative time of occurrence, where the cue and the shift stimulus for the first saccade in each of the experiments listed was the same or similar (S) or was different (D)

Experiment	Task Characteristics					No. of Diff. Features
	Brightness	Size	Fill	Shape	Time	
Pertsov '10	S	D	D	D	D	4
Mathôt '10	S	D	S	S	S	1
Exp. 1	D	D	D	S	S	3
Exp. 2	S	D	D	S	S	2

distinctiveness mediates the hypothetical retinotopic-to-spatiotopic remapping process. Our primary objective was to determine which factor may have led to significant retinotopic but insignificant spatiotopic IOR soon after an intervening eye movement was made in Mathôt and Theeuwes (2010)—a finding that, upon further scrutiny of their data, was questionable, and a finding that had, until our reanalysis, been in conflict with the findings of Pertsov et al. (2010). Recall that this particular finding, coupled with the findings of significant spatiotopic IOR but insignificant retinotopic IOR at longer CTOAs, led Mathôt and Theeuwes (2010) to the inference that spatiotopically coded IOR was derived from an initial retinotopically coded representation of IOR. We employed Mathôt and Theeuwes's (2010) quasirandom stimulus presentation procedure because it was possible that this methodological

aspect, unique to Mathôt and Theeuwes (2010), may have contributed to greater retinotopic than spatiotopic IOR at their short CTOA. Thus, we preserved this particular methodological feature (which may have delayed the onset of spatiotopic coding) and manipulated the other theoretically meaningful factor (i.e., cue-shift stimulus distinctiveness, which may also have delayed spatiotopic coding). Had we reproduced Mathôt and Theeuwes's (2010) reported finding in the present investigation, there would be relatively strong evidence against the featural-salience hypothesis, and we would, consequently, be justified in following the experiment up with a direct test of the locational-salience hypothesis. Our finding of evidence in favor of the locational-salience hypothesis (see Fig. 3) does not preclude the possibility that presenting Mathôt and Theeuwes's (2010) stimuli at fixed (instead of quasirandom) locations would increase the magnitude of spatiotopic IOR at the earliest CTOA. That noted, so long as one is willing to compare across experiments from different laboratories, the pattern in Fig. 3 argues against the locational-salience hypothesis: When cue-shift stimulus similarity was relatively low (see the data points for the three- and four-feature differences), we found almost as much IOR using variable locations as did Pertsov et al. (2010) using fixed locations.

Forward bias of saccades

The third finding from our experiments was a highly significant forward bias. Although this was seen, statistically, as a main effect of the coordinate space that we were testing, we believe that it is appropriate to measure this forward bias using only the baseline locations (to minimize the potential contributions of retinotopic and spatiotopic IOR). Measured in this way, the forward biases were 36 and 30 ms in Experiments 1 and 2, respectively. This forward bias could be caused by IOR left behind when gaze shifted to a new location (MacInnes & Klein, 2003), or it might instead have been an example of saccadic momentum (Smith & Henderson, 2009, 2011a, 2011b), a behavioral effect that may have its roots in the wiring diagram of the intermediate layers of the superior colliculus (Wang, Satel, Trappenberg, & Klein, 2011). A similar forward bias (21 ms) was present in Mathôt and Theeuwes (2010), but only at the shortest CTOA that they tested. Saccades directed to the uncued retinotopic and spatiotopic locations are not precisely forward and return saccades, respectively; rather, in polar coordinates, they are directed 45 deg away from the forward and return directions. Since IOR does not decay as rapidly as momentum, we tentatively assumed that the forward bias is an example of saccadic momentum and that this momentum effect is characterized by a gradient (as has been demonstrated, during viewing of complex scenes, by Smith & Henderson, 2009) that includes the forward target locations. Regardless, this effect is methodologically balanced across the cued and uncued locations used to calculate the cue-generated

Fig. 3 IOR scores as a function of cue-shift stimulus distinctiveness (see Table 2). Retinotopic IOR is plotted as open symbols, while spatiotopic IOR is plotted as filled symbols. The data from the shortest interval tested by Mathôt and Theeuwes (2010, as reanalyzed here; see the Appx.) are plotted as triangles, and those from Pertsov et al. (2010) are plotted as squares. Data from the present experiments are plotted as circles. The best-fitting linear functions regressing IOR against $\log_2$ (-number of different features) are shown for both spatiotopic (solid line) and retinotopic (dashed line) IOR scores

retinotopic and spatiotopic IOR scores that are the focus of this investigation.

Conclusions

While the debate on the link between retinotopic and spatiotopic representations of space remains largely unsettled (cf. Burr & Morrone, 2011; Hall & Colby, 2011; Mathôt & Theeuwes, 2011, for conflicting theoretical accounts), the primary objective of the present investigation was to resolve *when*, relative to an intervening saccadic eye movement, IOR would exist in spatiotopic coordinates. On this point, the pres-

ent and extant data on the dynamic remapping of oculomotor IOR are in good agreement: Cue-generated IOR exists in spatiotopic coordinates at the earliest possible behavioral measurement following a postcue saccade, a finding that is consistent with IOR's proposed function as a foraging facilitator.

Author note We are grateful to Sebastian Mathôt and Jan Theeuwes for sharing their data and code with us. We are also grateful to Yoni Pertzov, Ana Vivas, and an anonymous reader for constructive advice. Finally, we thank Julie Golomb for providing general assistance and guidance on the concept of dynamic remapping during the earlier stages of this research project. This research was made possible by an NSERC Graduate Scholarship to M.D.H. and an NSERC Discovery Grant to R.M.K.

Appendix

Fig. A1 Saccadic response time (SRT) distribution for all of the conditions of Mathôt and Theeuwes (2010). The dashed line shows the lower cutoff used by Mathôt and Theeuwes (2010), while the solid line shows the cutoff that we used in our reanalysis

Fig. A2 The IOR results from Mathôt and Theeuwes (2010) when target saccadic response times (SRTs) between 0 and 100 ms were excluded. The x-axis refers to the time between the achievement of fixating the shift stimulus and the onset of the target stimulus

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