

# Gradual Remapping Results in Early Retinotopic and Late Spatiotopic Inhibition of Return

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## Abstract

Here we report that immediately following the execution of an eye movement, oculomotor inhibition of return resides in retinotopic (eye-centered) coordinates. At longer postsaccadic intervals, inhibition resides in spatiotopic (world-centered) coordinates. These results are explained in terms of perisaccadic remapping. In the interval surrounding an eye movement, information is remapped within retinotopic maps to compensate for the retinal displacement. Because remapping is not an instantaneous process, a fast, but gradual, transfer of inhibition of return from retinotopic to spatiotopic coordinates can be observed in the postsaccadic interval. The observation that visual stability is preserved in inhibition of return is consistent with its function as a “foraging facilitator,” which requires locations to be inhibited across multiple eye movements. The current results support the idea that the visual system is retinotopically organized and that the appearance of a spatiotopic organization is due to remapping of visual information to compensate for eye movements.

## Keywords

remapping, inhibition of return, eye movements, visual attention, visual stability

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People perceive the world as being stable and are capable of making accurate, visually guided movements. This is remarkable considering the fact that visual perception relies on input from the retina, which, because of eye movements, is unstable. The apparent conflict between the lack of stability in visual input and the stable nature of conscious visual perception is often referred to as the problem of visual stability.

An intuitively appealing solution to this problem is to assume that only early visual areas are affected by eye movements. It is an old idea, often attributed to Helmholtz or even pre-Socratic philosophers, that information about eye position is crucial in maintaining visual stability (Grusser, 1986). The spatiotopic hypothesis posits that action and conscious perception are based on a world-centered (spatiotopic) representation, which is constructed by combining gaze-centered (retinotopic) maps with eye-position information. However, there is little empirical support for this hypothesis. The most convincing evidence so far has been provided by a functional magnetic resonance imaging (fMRI) study showing spatiotopic responses in the human middle temporal cortex (d’Avossa et al., 2007), but this finding has recently been contested (Gardner, Merriam, Movshon, & Heeger, 2008). The evidence is somewhat different for multimodal parietal areas, where

gaze-modulated visual receptive fields are frequently observed (Duhamel, Bremmer, BenHamed, & Graf, 1997; Galletti, Battaglini, & Fattori, 1993, 1995). However, there is ongoing debate about how these receptive fields are best characterized (Mullette-Gillman, Cohen, & Groh, 2005).

The fact that the visual system is largely retinotopically organized has caused many researchers to look beyond spatiotopy for mechanisms underlying visual stability (for recent reviews, see Mathôt & Theeuwes, in press; Wurtz, 2008). A mechanism that has received considerable interest is remapping of receptive fields (Duhamel, Colby, & Goldberg, 1992). According to the retinotopic (or remapping) hypothesis, information is transferred within retinotopic maps to compensate for eye movements. For example, consider a stimulus that is presented briefly and then extinguished, leaving some residual neural activity (i.e., a memory trace). If an eye movement is executed such that the former location of the stimulus is

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carried across the vertical meridian, there is a corresponding shift of neural activity from one hemisphere to the other, which can be measured using fMRI (Merriam, Genovese, & Colby, 2003). The effect of this interhemispheric remapping is that the memory trace does not become misaligned with the world after the eye movement. Therefore, in many ways, remapping gives the appearance of a spatiotopically organized visual system while relying on retinotopic maps.

A prime example of a phenomenon in which maintaining visual stability is crucial is inhibition of return (IOR). IOR refers to the fact that people tend not to revisit recently attended locations, either with their eyes or by a covert shift of attention (Posner & Cohen, 1984). IOR is often described as a “foraging facilitator” because it facilitates visual search by preventing observers from visiting the same locations over and over again, neglecting most of the visual field (Klein, 1988). Because IOR is a sustained effect that spans multiple eye movements, it would be maladaptive if it were tied to retinotopic coordinates. Indeed, a number of studies have shown that IOR resides in spatiotopic coordinates (Maylor & Hockey, 1985; Posner & Cohen, 1984; but see Abrams & Prat, 2000) and can be maintained across multiple eye movements (Klein & MacInnes, 1999). More recently, studies have shown that IOR has both a spatiotopic and a retinotopic component, but that the spatiotopic component can be disrupted by parietal lesions (Sapir, Hayes, Henik, Danziger, & Rafal, 2004) or the application of transcranial magnetic stimulation to the right parietal cortex (van Koningsbruggen, Gabay, Sapir, Henik, & Rafal, 2010). These findings clearly show that stability is somehow preserved in IOR, presumably by a process that involves the parietal cortex. However, the underlying mechanisms are still unclear.

In the study reported here, we investigated whether the spatiotemporal properties of IOR are consistent with the hypothesis that IOR relies on retinotopic maps and is remapped gradually in the perisaccadic interval. The retinotopic hypothesis predicts that a particular visual phenomenon may appear to be spatiotopic or retinotopic depending on the time of measurement because remapping is a process that takes time (Kusunoki & Goldberg, 2003): Remapping starts well before the onset of a saccade (Duhamel et al., 1992), but visual stability is not fully restored until some time after a saccade (e.g., Hamker, Zirnsak, Calow, & Lappe, 2008). A recent study by Golomb and her colleagues (Golomb, Chun, & Mazer, 2008) is of particular relevance here. They investigated how the reference frame of attentional facilitation, which typically precedes the inhibitory phase we investigated in this study, changes in the postsaccadic interval. In one experiment, they found retinotopic facilitation directly after a saccade and spatiotopic facilitation at longer intervals. However, in a second experiment, in which participants were asked to attend to a location “relative to their eyes,” no spatiotopic facilitation was found. This led the authors to conclude that the reference frame of visual attention is retinotopic, unless remapping is required to perform the task at hand. Although we agree that

visual attention relies on a retinotopically organized visual system, we have previously shown that the locus of attention is also remapped when attention is manipulated using a task-irrelevant onset stimulus (Mathôt & Theeuwes, 2010).

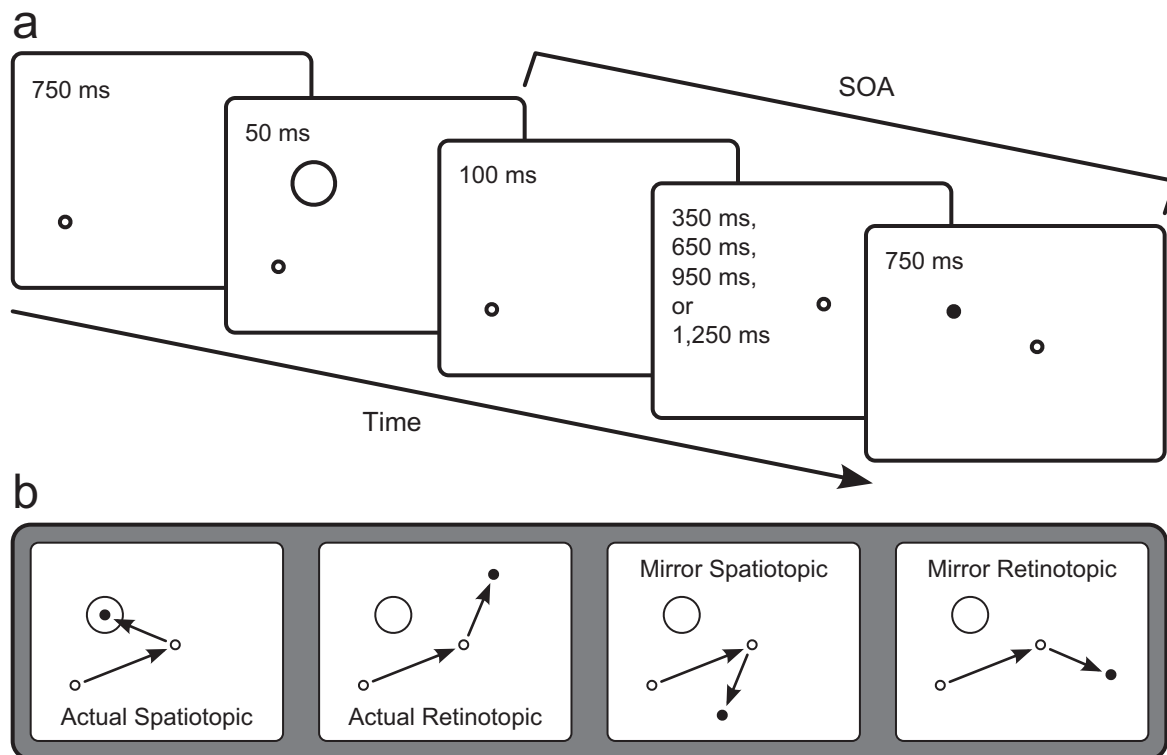
The aim of the study reported here was to investigate whether the reference frame of IOR changes in the postsaccadic interval, as has been shown for attentional facilitation (Golomb et al., 2008). We predicted that IOR is predominantly retinotopic when measured just after an eye movement. However, at a relatively long delay between the eye movement and the time of measurement, we expected IOR to be predominantly spatiotopic. To test this hypothesis, we briefly presented an onset stimulus in order to exogenously attract attention, which has been shown to elicit IOR at relatively long intervals ( $\geq 300$  ms; Posner & Cohen, 1984). Subsequently, participants made two eye movements. The first eye movement allowed us to dissociate spatiotopic and retinotopic coordinates. The latency of the second eye movement allowed us to determine the strength of IOR at the retinotopic and spatiotopic locations.

## Method

Thirteen naive observers and one of the authors (S.M.), all between the ages of 18 and 27 years, participated in the experiment. All participants reported normal or corrected visual acuity. Eye movements were recorded using an Eyelink II (SR-Research, Mississauga, Ontario, Canada), a video-based eye tracker, sampling at 1000 Hz.

Before the start of each trial, a gray cross was presented on a computer screen against a dark background. Drift correction was executed automatically when participants fixated this cross (except for the first trial of each block, in which a key press was required), after which the trial was initiated. Each trial started with the presentation of a gray fixation dot (see Fig. 1a). After 750 ms, an onset stimulus (an empty circle, diameter =  $0.5^\circ$ ) was presented to manipulate participants' attention. The onset stimulus was visible for 50 ms. After another 100 ms (and a total of 900 ms), the fixation dot was displaced  $6^\circ$  to a random location. Participants were instructed to follow the displacement with their eyes. After a variable interval (350 ms, 650 ms, 950 ms, or 1,250 ms), a saccade target (a green dot) was presented  $4.2^\circ$  from the fixation dot for 750 ms. Participants were instructed to make a saccade to the target as quickly as possible. The location of the saccade target was used as the starting location for the next trial.

Four trial types were created through the relative locations of the onset and target stimuli: The onset stimulus and the green saccade target could be presented at the same spatial location (actual spatiotopic trials), the same location relative to the fixation dot (actual retinotopic trials), or one of two comparable control arrangements (mirror spatiotopic and mirror retinotopic trials; see Fig. 1b). Stimulus arrangements were rotated randomly so that there was a mixture of trials in which the onset needed to be remapped across the vertical meridian



**Fig. 1.** Illustration of the trial sequence and experimental conditions. The schematic in (a) shows an example of an actual spatiotopic trial. Participants made two eye movements. The first eye movement followed the displacement of the fixation dot (small empty circle) and allowed us to dissociate retinotopic and spatiotopic coordinates. The second eye movement was to the green saccade target (small filled circle). We manipulated attention by briefly presenting an onset stimulus (large empty circle) prior to the eye movements. The stimulus onset asynchrony (SOA) was the time from the presentation of the onset stimulus to the presentation of the green saccade target. The schematic in (b) shows the four possible stimulus arrangements and the corresponding eye movements (represented by arrows). The saccade target could be presented at the onset location (actual spatiotopic trial), the location that retinotopically matched the onset location (actual retinotopic trial), or one of two control locations (mirror spatiotopic and mirror retinotopic trials). Stimulus arrangements were randomly rotated and positioned on the display.

and trials in which this was not the case. The stimulus onset asynchrony (SOA) between the presentation of the onset stimulus and the green saccade target varied as a result of the variable duration of the displaced fixation dot, resulting in SOAs of 500 ms, 800 ms, 1,100 ms, and 1,400 ms.

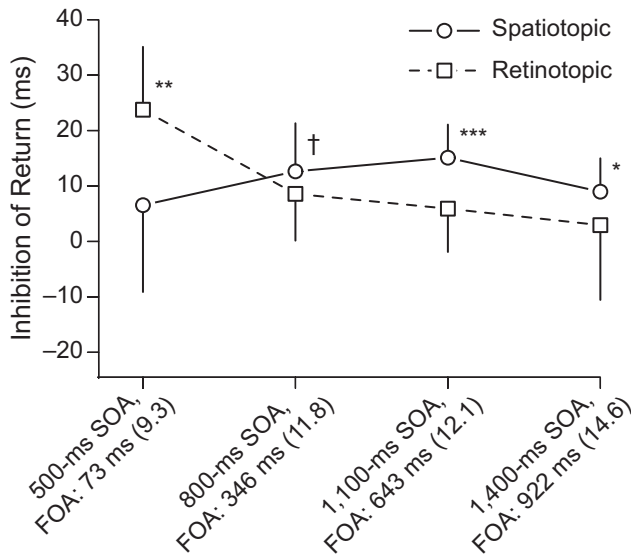
If gaze deviated more than  $2^\circ$  from the expected position during the experiment, the participant received auditory feedback and the trial was continued but discarded. The experiment consisted of 30 practice trials followed by 640 experimental trials.

## Results

Trials were excluded if participants' gaze deviated more than  $1^\circ$  from the initial fixation dot, more than  $2^\circ$  from the displaced fixation dot, or more than  $2^\circ$  from the saccade target, or if the required eye movements were not executed (22.2% of trials). The primary reason for gaze error was oculomotor capture by the onset stimulus, which accounted for about half of the errors, a value consistent with that observed in previous studies (Theeuwes, Kramer, Hahn, & Irwin, 1998). Trials in which the latency of the second saccade (to the saccade target) was less than 50 ms or more than 500 ms were also excluded

(4.7% of trials). The target of the second saccade was never presented prior to the initiation of the first saccade. In total, 74.2% of the trials were included in the analysis.

We conducted a repeated measures analysis of variance (ANOVA) with coordinate system (spatiotopic or retinotopic), saccade-target location (actual or mirror), and SOA as the independent variables and the latency of the second saccade (to the saccade target) as the dependent variable. The analysis revealed the following effects (see Fig. 2 and Table 1): a main effect of saccade-target location,  $F(1, 13) = 22.3, p < .001, \eta_p^2 = .63$ , reflecting an overall IOR effect (i.e., shorter latencies for mirror than for actual locations); a main effect of coordinate system,  $F(1, 13) = 8.0, p < .05, \eta_p^2 = .38$ , reflecting shorter latencies in retinotopic than in spatiotopic trials; a main effect of SOA,  $F(3, 13) = 10.0, p < .001, \eta_p^2 = .44$ , reflecting shorter latencies at higher SOAs; and an interaction between coordinate system and SOA,  $F(3, 39) = 4.15, p < .05, \eta_p^2 = .24$ , reflecting a more pronounced decrease in latency with increasing SOA for the spatiotopic trials than for the retinotopic trials. Crucially, we also found a three-way interaction of coordinate system, saccade-target location, and SOA,  $F(3, 39) = 3.4, p < .05, \eta_p^2 = .21$ , reflecting the different time courses for retinotopic and spatiotopic IOR.



**Fig. 2.** Inhibition of return as a function of coordinate system and stimulus onset asynchrony (SOA). Inhibition of return was measured as latency of the second saccade when the target was at the actual location minus latency of the second saccade when the target was at the mirror location (see Fig. 1b). The mean fixation onset asynchrony (FOA; with standard error in parentheses) for each SOA is provided along the x-axis. FOA is the time from the end of the first saccade to the presentation of the saccade target. Asterisks denote significant inhibition of return ( $^{\dagger}p < .1$ ,  $^*p < .05$ ,  $^{**}p < .01$ ,  $^{***}p < .005$ ). Error bars represent 95% within-subjects confidence intervals (Cousineau, 2005). Overlapping portions of the error bars have been removed for clarity.

Planned comparisons revealed significant IOR (increased saccade latencies to the actual, relative to the mirror, locations) for the retinotopic trials when the SOA was 500 ms (actual:  $M = 260$  ms,  $SE = 12.7$ ; mirror:  $M = 236$  ms,  $SE = 15.5$ ),  $t(13) = 3.3$ ,  $p < .01$ , and for the spatiotopic trials when the SOA was 1,100 ms (actual:  $M = 230$  ms,  $SE = 10.8$ ; mirror:  $M = 215$  ms,  $SE = 10.6$ ),  $t(13) = 3.6$ ,  $p < .005$ , or 1,400 ms (actual:  $M = 226$  ms,  $SE = 9.4$ ; mirror:  $M = 217$  ms,  $SE = 8.1$ ),  $t(13) = 2.8$ ,  $p < .05$ . There was a marginally significant spatiotopic IOR effect at the 800-ms SOA (actual:  $M = 253$  ms,  $SE = 10.7$ ; mirror:  $M = 240$  ms,  $SE = 12.7$ ),  $t(13) = 2.2$ ,  $p = .05$ .

Because our main goal was to investigate how the reference frame of IOR changes in the postsaccadic interval, we

determined the time between the end of the first saccade and the presentation of the target for the second saccade. The average fixation onset asynchrony (FOA) was 73 ms ( $SE = 9.3$ ) for the 500-ms SOA, 346 ms ( $SE = 11.8$ ) for the 800-ms SOA, 634 ms ( $SE = 12.1$ ) for the 1,100-ms SOA, and 922 ms ( $SE = 14.6$ ) for the 1,400-ms SOA. Thus, there was retinotopic IOR on average 73 ms after the end of the first saccade, and there was spatiotopic IOR on average 634 ms and 922 ms after the first saccade.

## Discussion

This study shows that the spatiotemporal properties of IOR are consistent with the idea that IOR relies on retinotopic maps and that information in these retinotopic maps is remapped gradually during the perisaccadic interval. Only at the shortest interval, on average 73 ms after the eye movement (500 ms after the presentation of the onset), was there IOR at the location that retinotopically matched the onset location. IOR at the original onset (spatiotopic) location was found at longer postsaccadic intervals. This finding illustrates that remapping of the locus of IOR is a gradual process that persists into the postsaccadic interval.

This study complements the existing literature in a number of ways. Most support for remapping has been obtained in neurophysiological (e.g., Duhamel et al., 1992; Kusunoki & Goldberg, 2003) and neuroimaging (e.g., Merriam et al., 2003; Parks & Corballis, 2008) studies. Studies that have employed behavioral methods have generally focused on the presaccadic interval (Hunt & Cavanagh, 2009; Mathôt & Theeuwes, 2010; Melcher, 2007) or have addressed the reference frame of visual phenomena without directly investigating their dynamic nature (e.g., Ezzati, Golzar, & Afraz, 2008; Knapen, Rolfs, & Cavanagh, 2009). Here, we have shown that the reference frame of IOR is highly dynamic, as has been shown previously for attentional facilitation (Golomb et al., 2008).

Recently, Pertzov, Zohary, and Avidan (in press) reported strong spatiotopic IOR immediately after a saccade. This finding is surprising given the study by Golomb et al. (2008) and the study reported here, which suggest that remapping of attentional effects (facilitation as well as IOR) is not yet complete at the time a saccade is finished. This apparent discrepancy warrants further scrutiny.

**Table 1.** Saccade Latencies and Inhibition of Return for Each Stimulus Onset Asynchrony

Stimulus onset asynchrony	Spatiotopic coordinate system			Retinotopic coordinate system		
	Actual location	Mirror location	IOR	Actual location	Mirror location	IOR
500 ms	272	265	7	260	236	24**
800 ms	253	240	13 <sup>†</sup>	247	238	9
1,100 ms	230	215	15***	225	219	6
1,400 ms	226	217	9*	217	214	3

Note: All values are in milliseconds. Inhibition of return (IOR) was calculated by subtracting mean saccade latency in the mirror location from mean saccade latency in the actual location.

<sup>†</sup> $p < .1$ .  $^*p < .05$ .  $^{**}p < .01$ .  $^{***}p < .005$ .

Given the assumption that remapping is predictive—that is, occurring before, instead of after, a saccade—the current findings may be surprising. However, we believe that the results of our study complement rather than challenge the notion of predictive remapping. Although we did not find significant spatiotopic IOR at the early postsaccadic intervals, we do not contest that early spatiotopic effects can be observed in different experimental paradigms (e.g., Mathôt & Theeuwes, 2010). The crucial finding here is that even after an eye movement has ended, it takes some time for spatiotopic IOR to be fully restored (see also Golomb et al., 2008). Therefore, we prefer to use the term remapping not only for presaccadic processes, but for all perisaccadic processes that allow for a translation from retinotopic to spatiotopic coordinates.

Given the presumed role of IOR as a foraging facilitator and the fact that IOR typically spans multiple eye movements, one would not expect IOR to be purely retinotopic: It would be maladaptive to inhibit a novel location that happens to be in the same retinal position as a previously visited location. Consistent with this functional view, findings from previous studies indicate that IOR resides in spatiotopic coordinates (Klein & MacInnes, 1999; Maylor & Hockey, 1985; Posner & Cohen, 1984). However, our study shows that spatiotopy is not a fundamental property of IOR, but instead emerges through the active process of remapping. An alternative explanation would be that our findings do not reflect a remapping of the locus of IOR per se, but rather remapping of the locus of attention, with the transition from facilitation to inhibition occurring after the first saccade. However, this is highly unlikely given the short interval (on average, 73 ms) between the end of the first saccade and the earliest time at which the target for the second saccade was presented, given that the transition from facilitation to inhibition takes at least 200 ms (e.g., Posner & Cohen, 1984).

In summary, the present study shows that the locus of IOR is remapped in the postsaccadic interval. After an eye movement, there is a narrow temporal window during which visual stability has not yet been fully restored. During this period, the retinotopic nature of the visual system can be exposed. At longer postsaccadic intervals, remapping has largely compensated for the eye movement, thus giving the appearance of spatiotopy at a behavioral level, even though the underlying system is retinotopically organized.

### Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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