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

Sebastiaan Mathôt & Jan Theeuwes

Vrije Universiteit, Amsterdam, The Netherlands

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 post-saccadic intervals inhibition resides in spatiotopic (world-centered) coordinates. These results are explained in terms of peri-saccadic 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 post-saccadic 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

We 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 an 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 situation is somewhat different in multimodal parietal areas, where gaze modulated visual receptive fields (RFs) are frequently observed (Duhamel, Bremmer, BenHamed, & Graf, 1997; Galletti, Battaglini, & Fattori, 1993, 1995). However, there is ongoing debate about how these RFs 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 which has received considerable interest is remapping of RFs (Duhamel, Colby, & Goldberg, 1992). According to the retinotopic (or remapping) hypothesis information is transferred within retinotopic maps to compensate for eye movements. Consider, for example, a stimulus which is presented briefly and then extinguished, leaving some residual neural activity. If an eye movement is executed such that the former stimulus location is 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 inter-hemispheric 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 us from visiting the same locations over and over again, while neglecting most of the visual field (Klein, 1988). Because IOR is a sustained effect, spanning 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 retinotopic component, but that the spatiotopic component can be disrupted by parietal lesions (Sapir, Hayes, Henik,

Danziger, & Rafal, 2004) or the application of TMS 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 which involves the parietal cortex. However, the underlying mechanisms are still unclear.

In the present study 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 peri-saccadic 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 which 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 sometime after a saccade (e.g., Hamker, Zirnsak, Calow, & Lappe, 2008). A recent study by Golomb and colleagues (Golomb, Chun, & Mazer, 2008) is of particular relevance here. Golomb and colleagues investigated how the reference frame of attentional facilitation, which typically precedes the inhibitory phase investigated here, changes in the post-saccadic interval. In one experiment they showed 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. While 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).
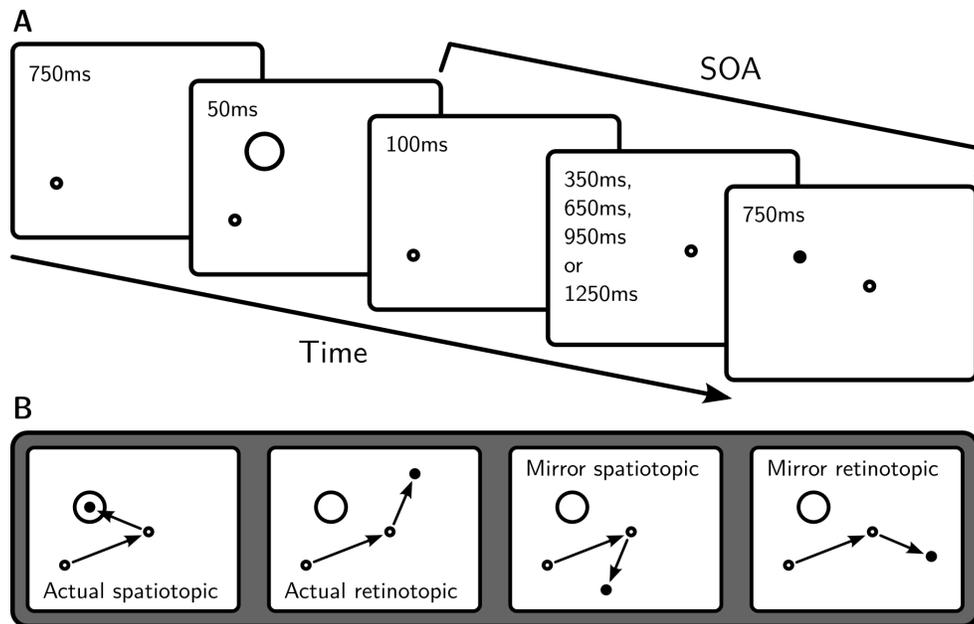
Figure 1. A) A schematic example trial in the 'actual spatiotopic' condition. Participants made two eye movements. The first eye movement matched the displacement of the fixation dot (small empty circle) and allowed us to dissociate retinotopic and spatiotopic coordinates. The second eye movement was to the green saccade target (small filled circle). We manipulated attention by briefly presenting an onset stimulus (large empty circle). B) The four possible stimulus arrangements and corresponding eye movements (arrows). The saccade target could be presented at the onset location (actual spatiotopic), the location which retinotopically matched the onset location (actual retinotopic) or at one of two control locations (mirror spatiotopic and mirror retinotopic). Stimulus arrangements were randomly rotated and positioned on the display.

The aim of the present study was to investigate whether the reference frame of IOR changes in the post-saccadic 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. If the delay between the eye movement and the time of measurement is relatively long, we expected IOR to be predominantly spatiotopic. To test this hypothesis we briefly presented an onset stimulus in order to exogenously attract attention, eliciting IOR at longer intervals (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 (SM), all between the ages of 18 and 27, participated in the experiment. All participants reported normal or corrected visual acuity. Eye movements were recorded using an Eyelink II (SR-Research), a video-based eye-tracker sampling at 1000Hz.

Before the start of each trial a gray cross was presented against a dark background. Drift-correction was executed automatically when participants fixated this cross (except for in the first trial of each block in which a

keypress was required), after which the trial was initiated. Each trial started with the presentation of a gray fixation dot (see Figure 1A). After 900ms, the fixation dot was displaced 6° to a random location. Participants followed the displacement with their eyes. After a variable interval (350ms, 650ms, 950ms or 1250ms) a saccade target (a green dot) was presented 4.2° from the fixation dot for 750ms. Participants made 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.

Attention was manipulated by the presentation of an onset stimulus (an empty circle, d = 0.5°) for 50ms, 150ms prior to the displacement of the fixation dot. The onset stimulus and the green saccade target were presented at the same spatial location (actual spatiotopic; see Figure 1B), the same location relative to the fixation dot (actual retinotopic), or in one of two comparable control arrangements (mirror spatiotopic and mirror retinotopic). Stimulus arrangements were rotated randomly so that there was a mixture of trials in which the onset location needed to be remapped across the vertical meridian and trials in which this was not the case.

If gaze deviated more than 2° 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 in which gaze deviated more than 1° from the initial fixation dot, more than 2° from the displaced fixation dot, more than 2° from the saccade target, or in which the required eye movements were not executed, were excluded (22.2%). The primary reason for gaze error was oculomotor capture by the onset, which accounted for about half of these errors, consistent with previous studies (Theeuwes, Kramer, Hahn, & Irwin, 1998). Trials in which the latency

of the second saccade (to the saccade target) was less than 50ms or more than 500ms were excluded (4.7%). 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.

A repeated measures analysis of variance (ANOVA) with condition (spatiotopic or retinotopic), location (actual or mirror) and stimulus onset asynchrony (SOA; the interval between the presentation of the onset stimulus and the saccade target; 500ms, 800ms, 1100ms or 1400ms) as independent variables and the latency of the second saccade (to the saccade target) as dependent variable revealed the following effects (see Figure 2 and Table 1): a main effect of location ($F(1, 13) = 22.3$, $p < .001$, $\eta_p^2 = .63$), reflecting an overall IOR effect; a main
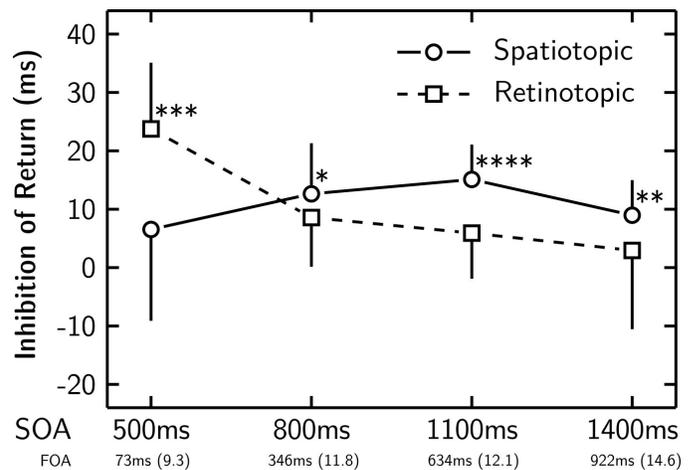
Figure 2. The results of the experiment. 500ms after the presentation of the onset (SOA) and on average 73ms after the end of the first saccade (FOA) there was retinotopic IOR. At 1100ms SOA (634ms FOA) and 1400ms SOA (922ms FOA) there was spatiotopic IOR. The FOA standard error is provided within parentheses. IOR was measured as an increased saccade latency of the second saccade to the actual, relative to the mirror locations (see Figure 1B). Asterisks denote significant IOR (*p < .1, **p < .05, ***p < .01, ****p < .005). Error bars represent a 95% within-subject confidence interval (Cousineau, 2005). Overlapping error bars have been removed for clarity.

Table 1.

An Overview of Reaction Times (ms) per Condition

SOA (ms)	Spatiotopic			Retinotopic		
	Actual	Mirror	IOR	Actual	Mirror	IOR
500	272	265	7	260	236	24***
800	253	240	13*	247	238	9
1100	230	215	15****	225	219	6
1400	226	217	9**	217	214	3

Note. *p < .1, **p < .05, ***p < .01, ****p < .005

effect of condition ($F(1, 13) = 8.0$, $p < .05$, $\eta_p^2 = .38$), reflecting lower latencies in the retinotopic, relative to the spatiotopic condition; a main effect of SOA ($F(3, 13) = 10.0$, $p < .001$, $\eta_p^2 = .44$), reflecting lower latencies at higher SOAs; an interaction between condition and SOA ($F(3, 39) = 4.15$, $p < .05$, $\eta_p^2 = .24$), reflecting a more pronounced latency decrease with increasing SOA for the spatiotopic condition. Crucially, we also found a three-way interaction between condition, location and SOA ($F(3, 39) = 3.4$, $p < .05$, $\eta_p^2 = .21$), reflecting the different time course for retinotopic and spatiotopic IOR.

Planned comparisons revealed IOR (as measured by increased saccade latencies to the actual, relative to the mirror locations) for the retinotopic condition at 500ms SOA (actual: $M = 260$ms, $SE = 12.7$; mirror: $M = 236$ms, $SE = 15.5$; $t(13) = 3.3$, $p < .01$), and for the spatiotopic condition at the 1100ms (actual: $M = 230$ms, $SE = 10.8$; mirror: $M = 215$ms, $SE = 10.6$; $t(13) = 3.6$, $p < .005$) and 1400ms SOAs (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 800ms 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 post-saccadic 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) in the 500ms SOA was 73ms ($SE = 9.3$), 346ms ($SE = 11.8$) in the 800ms SOA, 634ms ($SE = 12.1$) in the 1100ms SOA and 922 ($SE = 14.6$) in the 1400ms SOA.

Discussion

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

The present study complements 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 studies (e.g., Merriam, Genovese, & Colby, 2003; Parks & Corballis, 2008). Studies which have employed behavioral methods have generally focused on the pre-saccadic 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 show that the reference frame of IOR is highly dynamic, as has been

shown previously for attentional facilitation (Golomb et al., 2008).

Recently, Pertzov and colleagues (Pertzov, Zohary, & 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 present study, 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.

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 present study complements rather than challenges the notion of predictive remapping. Although we did not find significant spatiotopic IOR at the early post-saccadic 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 pre-saccadic processes, but for all peri-saccadic processes which 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 which happens to be in the same retinal position as a previously visited location. Consistent with this functional view, previous studies have shown that IOR resides in spatiotopic coordinates (Klein & MacInnes, 1999; Maylor & Hockey, 1985; Posner & Cohen, 1984). However, the present study shows that spatiotopy is not a fundamental property of IOR, but emerges through the active process of remapping. An alternative explanation would be that the current findings do not reflect remapping of IOR per sé, 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 73ms) between the end of the first saccade and the earliest time of measurement, since the transition from facilitation to inhibition takes at least 200ms (e.g., Posner & Cohen, 1984).

In summary, the present study shows that the locus of IOR is remapped in the post-saccadic 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 post-saccadic intervals, remapping has largely compensated for the eye movement, thus giving, at a behavioral level, the appearance of spatiotopy, while relying on a retinotopically organized visual system.

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