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The Effect of Saccadic Response Time on the Reference Frame of Inhibition of Return

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Author Note

Abstract

We have previously shown that oculomotor inhibition of return is predominantly retinotopic (gaze-centred) immediately following a saccadic eye movement, and predominantly spatiotopic (world-centred) at longer post-saccadic delays (Mathôt & Theeuwes, 2010a). This claim has been contested by Hilchey et al. (2012), who re-analysed our data after removing very fast saccades (<100ms) and observed that removing these saccades attenuated the effect of interest. Here we report an elaborate re-analysis of that same dataset. We show that recent conflicting reports on the reference frame of inhibition of return can likely be reconciled by a previously unrecognised effect of saccadic response time. Oculomotor inhibition of return is predominantly retinotopic at short post-saccadic delays, particularly for fast saccades. In contrast, oculomotor inhibition of return is predominantly spatiotopic at longer post-saccadic delays, particularly for slow saccades. With respect to previous studies, differences in paradigm and trial exclusion criteria may have resulted in different distributions of saccadic response times, thus leading to different conclusions regarding the reference frame of inhibition of return. Finally, we argue that the effects reported here are not specific to inhibition of return, but reflect general mechanisms that are observed across a wide range of attentional, visuomotor, and visuotactile phenomena.

The Effect of Saccadic Response Time on the Reference Frame of Inhibition of Return

When attention is directed to a location and subsequently withdrawn, people are slower to respond manually to stimuli presented at that location (Posner & Cohen, 1984), and slower to make an eye movement to that location (Abrams & Dobkin, 1994; Klein & MacInnes, 1999; for a review, see Klein, 2000). This phenomenon is called inhibition of return (IOR), and is often interpreted as a 'been there, done that' mechanism, or foraging facilitator, that prevents us from revisiting the same locations over and over again. IOR thus facilitates visual search (Klein, 1988) and, presumably, our daily life interactions with our visual environment. Assuming that IOR serves this purpose, one would expect the locus of IOR to be tied to spatiotopic (world-centred) coordinates: Regardless of the current position of gaze, the same location 'out there' should be inhibited. It would make little sense for IOR to be tied to retinotopic (gaze-centred) coordinates, thus arbitrarily shifting around with each eye movement. This line of reasoning is supported by studies showing that IOR spans multiple eye movements (Klein & MacInnes, 1999; but see Ludwig, Farrell, Ellis, & Gilchrist, 2009) and is indeed, at least in part, tied to a spatiotopic frame of reference (Hilchey, Klein, Satel, & Wang, 2012; Mathôt & Theeuwes, 2010a; Maylor & Hockey, 1985; Pertzov, Zohary, & Avidan, 2010; Posner & Cohen, 1984; Sapir, Hayes, Henik, Danziger, & Rafal, 2004; van Koningsbruggen, Gabay, Sapir, Henik, & Rafal, 2010). In other words, IOR is largely robust to eye movements—as it should be.

We recently investigated the reference frame of IOR in more detail (Mathôt & Theeuwes, 2010a). Consistent with previous reports, we found that IOR has both a retinotopic and a spatiotopic component (Hilchey et al., 2012; Pertzov et al., 2010; Sapir et al., 2004). However, crucially, we also found a difference in the time-course of retinotopic and spatiotopic IOR.

Retinotopic IOR was strongest immediately after a saccadic eye movement (at short post-saccadic delays), but dissipated quickly. In contrast, spatiotopic IOR was more sustained and even appeared to increase at longer post-saccadic delays (this latter effect was not as pronounced, but see e.g. Golomb, Marino, Chun, & Mazer, 2011). We interpreted this as reflecting a 'remapping' mechanism that restores spatiotopic IOR after an eye movement, but leaves a transient retinotopic trace (cf. Golomb, Chun, & Mazer, 2008; Mathôt & Theeuwes, 2010b). This result is important because it helps to understand how spatiotopic IOR, and presumably other spatiotopic visual phenomena as well, emerge from a visual system that is by-and-large retinotopically organised (Golomb & Kanwisher, in press; Talbot & Marshall, 1941; for recent reviews, see Mathôt & Theeuwes, 2011; Wurtz, 2008).

However, in a recent paper, Hilchey, Klein, Satel, and Wang (2012) re-analysed our dataset (from Mathôt & Theeuwes, 2010a available from the first author's website) and came to an altogether different conclusion. Specifically, they excluded all saccadic responses that were faster than 100ms (1.4 standard deviations below the mean), whereas we had used a more conservative lower bound of 50ms (2.0 standard deviations below the mean). According to Hilchey and colleagues (2012), a lower bound of 100ms was more appropriate, because they considered faster saccades to be of little theoretical significance. Furthermore, visual inspection of the saccade latency distribution appeared to indicate that saccades faster than 100ms were outliers (see Fig A1 from Hilchey et al., 2012). After filtering the data based on this new exclusion criterion, Hilchey and colleagues (2012) found that the retinotopic component of IOR was substantially attenuated, particularly for the shortest SOA at which this component was strongest. Consequently, the difference in time-course, which was central to our story, was no longer

obvious. Based on this, Hilchey and colleagues (2012) concluded that our claim of early retinotopic and late spatiotopic IOR was based on an artefactual result, due to the inclusion of theoretically uninteresting "impossibly fast" saccades. They were strengthened in this conclusion by the fact that their re-analysis brought our results more in line with their own results (Hilchey et al., 2012) and those of Pertzov, Zohary, and Avidan (2010).

The aim of the present paper is two-fold. First, we want to share an elaborate re-analysis of that same dataset (from Mathôt & Theeuwes, 2010a). We have characterised a previously unrecognised, but crucial, effect of saccade latency (saccadic response time) on the reference frame of IOR. Specifically, retinotopic IOR is most pronounced for fast saccadic responses, whereas spatiotopic IOR is most pronounced for slow responses. We will show that by taking saccade latency into account, the dissociation between retinotopic and spatiotopic IOR becomes even more conspicuous—Unlike suggested by Hilchey and colleagues (2012), this dissociation is a robust phenomenon. However, our re-analysis does call for a modification, or rather extension, of our original interpretation (cf. Mathôt & Theeuwes, 2010a): IOR is predominantly retinotopic immediately after an eye movement, *particularly so for fast saccadic responses*, and predominantly spatiotopic at longer post-saccadic delays, *particularly so for slow saccadic responses*. Thus, the dominant reference frame of IOR is determined by both the speed of the saccadic response (saccade latency) and the time at which the saccade target is presented relative to a preceding eye movement (post-saccadic delay).

Second, we aim to refocus the debate on the central issue, which is one of timing. Hilchey and colleagues (2012) did not include a timing manipulation in their own experiment, in which the saccade target was always presented immediately following an eye movement. However, the

central issue is emphatically not the absolute strength of retinotopic and spatiotopic IOR at any single point in time. Although we did not ourselves find significant spatiotopic IOR immediately after a saccade, we explicitly avoided the implication that early spatiotopic effects do not exist (Mathôt & Theeuwes, 2010a, p. 1797). Instead, the central issue is the differential time-course of retinotopic and spatiotopic IOR: The finding that (according to our results) retinotopic IOR decays rapidly after a saccadic eye movement, whereas spatiotopic IOR is sustained and appears to increase somewhat with longer post-saccadic delays. In our view, this differential time-course is evidence for what we have referred to as 'gradual remapping', or the notion that visual stability is not fully restored until sometime (±150ms) after an eye movement. Here we re-assert this claim, and extend it by describing the (complementary) effect of saccade latency on the reference frame of IOR.

Methods

We present a novel analysis of a previously reported dataset. The full methods are described in Mathôt and Theeuwes (2010a). Here we briefly highlight the most important properties of the experiment, which was a variation on the double-step paradigm (Figure 1). While participants looked at a fixation dot, a task-irrelevant cue was briefly (50ms) presented to exogenously attract attention and elicit IOR at later post-cue intervals. 100ms after cue-offset, the fixation dot was displaced. Participants followed the displacement of the fixation dot with their eyes (saccade step 1). Next, after a variable interval, a saccade target appeared. Participants made a saccadic eye movement to the target (saccade step 2). The saccade target appeared at the same retinotopic location as the cue (actual retinotopic), the same spatial location as the cue (actual spatiotopic), or one of two control locations (mirror retinotopic, mirror spatiotopic). The total interval between

the onset of the cue and the onset of the saccade target (stimulus onset asynchrony; SOA) was

500ms, 800ms, 1100ms, or 1400ms. The interval between offset of the step 1 saccade and the

onset of the step 2 saccade target (post-saccadic delay) was respectively 73ms, 346ms, 634ms,

and 922ms for the different SOAs. For our purpose, the post-saccadic delay is of particular

theoretical interest, because it corresponds to the amount of time that the visual systems has to

'recover' from the preceding saccade. The latency of the step 2 saccade was the measure of

interest (referred to simply as saccade latency). IOR was defined as the difference in saccade

latency between actual and mirror trials.

<div align="center">Analysis</div>

After data pre-processing as described in Mathôt and Theeuwes (2010a), trials were divided

into bins based on saccade latency, separately for each combination of subject ($N = 14$),

coordinate system (spatiotopic, retinotopic), and saccade target location (actual, mirror). Separate

analyses were conducted across all SOAs (using 25 bins; Figure 2a), and for each SOA

separately (using 10 bins; Figure 2b)[1]. For each saccade latency bin, we calculated Bayes factors

(Bfs), based on the *retinotopic IOR – spatiotopic IOR* contrast, and the *spatiotopic IOR –*

retinotopic IOR contrast, to investigate whether there was a difference between retinotopic and

spatiotopic IOR and, if so, in which direction. We assumed a uniform distribution, a lower bound

of 0ms and an upper bound of 50ms. These bounds were chosen because the effect of IOR tends

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1   Because of the large variation of saccade latencies between subjects and, to a lesser extent, between conditions,

   the distributions of saccade latencies in adjacent bins overlap (Figure 2a,b). Therefore, it is difficult to pinpoint

   precisely at which saccade latencies retinotopic and spatiotopic IOR become dominant. Looking at data from

   individual subjects (not shown), it is clear that there is substantial variation in this respect, although the general

   effect of saccade latency is evident in almost every subject.

to be in the 0 to 50ms range (e.g., Hilchey et al., 2012; Klein, 2000; Mathôt & Theeuwes, 2010a; Pertzov et al., 2010; Posner & Cohen, 1984). (The effects reported here are not crucially dependent on the exact bounds and number of bins.) We considered only series of at least two consecutive bins that showed "substantial evidence" for a difference in one contrast (Bf > 3; cf. Jeffreys, 1961; reproduced in Wetzels et al., 2011).

The analysis employed here is unconventional, but appropriate for two reasons. First, when conducting a large number of post-hoc comparisons, a Bayesian approach is preferable to null hypothesis testing (Dienes, 2011). Second, our criteria were conservative, because "substantial evidence" following Jeffrey's (1961) criterion is more stringent than the commonly used alpha level of .05 (Wetzels et al., 2011), and we furthermore considered only series of at least two bins that showed substantial evidence for a difference in the same direction.

Discussion and results

It is clear that there is a large effect of saccade latency on the reference frame of IOR when considered across all SOAs (Figure 2a,c). For fast saccadic responses (approx. <150ms) retinotopic IOR is larger than spatiotopic IOR, whereas this pattern reverses for slow saccades (approx. >250ms)[1]. For saccades of intermediate latency there is no clear difference between spatiotopic and retinotopic IOR. The effect of saccade latency may explain why recent investigations of the reference frame of IOR have led to seemingly conflicting results (Hilchey et al., 2012; Mathôt & Theeuwes, 2010a; Pertzov et al., 2010). More specifically, this explains why early retinotopic IOR may be attenuated (relative to our findings) when strict trial exclusion criteria are applied (<100ms, cf. Hilchey et al., 2012; <150ms, cf. Pertzov et al., 2010) or when there is a low incidence of very fast saccades (as reported by Hilchey et al., 2012).

An obvious question is whether the effects of saccade latency and post-saccadic delay (manipulated through SOA in our experiment) have been confounded in the past. Could the effect of post-saccadic delay that we previously reported (Mathôt & Theeuwes, 2010a) have been an indirect effect of saccade latency? However, looking at Figure 2b, it appears that both effects are distinct (see also Table 1 from Mathôt & Theeuwes, 2010a), because it is not the case that the strongest retinotopic IOR is observed in the condition that elicited, on average, the fastest saccades. Rather, the data is best characterized as follows: IOR is predominantly retinotopic for fast saccadic responses at short post-saccadic delays, and predominantly spatiotopic for slow saccades at long post-saccadic delays (notably 634ms[2]).

The present results, although new within the context of IOR, are entirely consistent with the broader literature on remapping for visual stability. It appears that the same factors that determine the reference frame of IOR also determine the reference frame of many other attentional, visuomotor, and visuotactile phenomena (Azanón, Longo, Soto-Faraco, & Haggard, 2010; Azañón & Soto-Faraco, 2008; Blohm, Missal, & Lefevre, 2005; Golomb et al., 2008, 2011; Overvliet, Azañon, & Soto-Faraco, 2011). Most directly relevant here are the studies by Golomb and colleagues (2008, 2011), in which it was shown that attentional facilitation is predominantly retinotopic immediately following an eye movement, and predominantly spatiotopic at longer post-saccadic delay. This clearly resembles the effect of post-saccadic delay that we observed for IOR (Mathôt & Theeuwes, 2010a). Furthermore, the effect of saccade latency is consistent with a study by Blohm and colleagues (2005) on memory guided saccades.

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2   It is not entirely clear why the difference between spatiotopic and retinotopic IOR for slow saccades has largely vanished at the 1400ms SOA/ 922ms post-saccadic delay (although it is still quantitatively present). Possibly, this is because the general IOR effect is dissipating at this point in time.

They found that fast memory guided saccades are predominantly directed at the retinotopic location of a memorised target, whereas slow saccades are predominantly directed at the actual, spatiotopic location of a target. Remarkably, a study by Overvliet and colleagues (2011) suggests that these effects extend even to visuotactile remapping (i.e., the remapping from an anatomical to a world-centred frame of reference). In their study, participants made a saccadic eye movement to a hand that received tactile stimulation, while (in the crucial condition) their hands were crossed. Their findings parallel the results reported here: The eyes tended to go to the incorrect (anatomical) side when the delay between the tactile stimulation and the saccade cue was short (see also Azanón et al., 2010; Azañón & Soto-Faraco, 2008) and when the saccadic response was fast. We therefore believe that the present results should not be understood solely in the context of IOR, but in the broader context of the coordinate transformations that, among other things, underlie visual stability (Mathôt & Theeuwes, 2011).

From a neurophysiological point of view, we believe that the distinct pathways hypothesis favoured by Blohm and colleagues (2005) offers a plausible framework to accommodate the present results, particularly the effect of saccade latency. They suggest that very fast saccades are driven by a direct sub-cortical pathway that relies on a 'raw' representation of the environment (Krauzlis & Stone, 1999; Munoz & Wurtz, 1992). This representation is retinotopic for visual input (Blohm et al., 2005), anatomical for tactile input (Azañón & Soto-Faraco, 2008; Overvliet et al., 2011), and more generally reflects the native frame of reference of the input modality. In contrast, slow saccades are mediated by the same parietal and frontal cortical areas that have been implicated in remapping and thus rely on spatially updated representations (Duhamel, Colby, & Goldberg, 1992; Morris, Kubischik, Hoffmann, Krekelberg, & Bremmer, 2012; Sapir et

al., 2004; van Koningsbruggen et al., 2010). According to this view, the extent to which IOR is retinotopic or spatiotopic depends, at least in part, on the extent to which direct and indirect pathways are involved in the generation of the response.

In summary, we have shown that oculomotor IOR is predominantly retinotopic (gaze-centred) immediately following an eye movement, but particularly for fast saccadic responses, and predominantly spatiotopic (world-centred) at longer intervals after an eye movement, but particularly for slow saccadic responses. This complements our previous report (Mathôt & Theeuwes, 2010a) by showing that the reference frame of IOR depends not only on the time at which the saccade target is presented relative to a preceding eye movement (post-saccadic delay), but also on the speed of the saccadic response (saccade latency). We have stressed that our claim should not be taken to mean that early spatiotopic effects do not exist, but that there is a pronounced difference in the time-course of retinotopic and spatiotopic IOR. Furthermore, the effect of saccade latency on the reference frame of IOR potentially reconciles seemingly conflicting reports (Hilchey et al., 2012; Mathôt & Theeuwes, 2010a; Pertzov et al., 2010): Differences in paradigm and trial exclusion criteria may have resulted in different distributions of saccade latencies, in turn affecting the relative strength of retinotopic and spatiotopic IOR. We have suggested that different pathways may be involved in fast and slow saccadic eye movements, relying respectively on retinotopic and remapped (behaviourally spatiotopic) representations (Blohm et al., 2005; Krauzlis & Stone, 1999; Munoz & Wurtz, 1992). Finally, we have argued that the present results are likely not limited to IOR, but extend to many attentional, visuomotor, and visuotactile phenomena.

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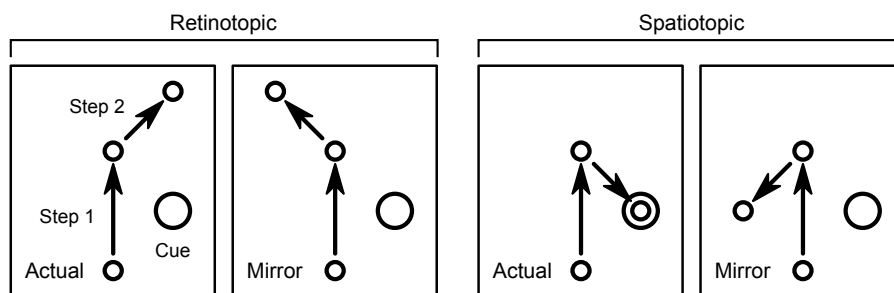Hilchey, M. D., Klein, R. M., Satel, J., & Wang, Z. (2012). Oculomotor inhibition of return: How

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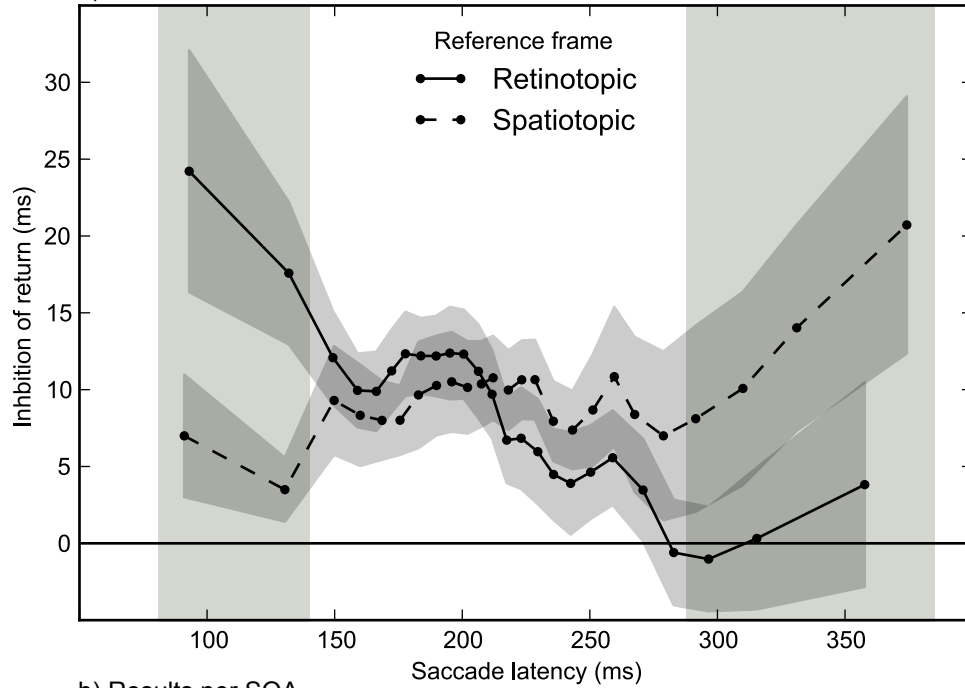Wurtz, R. H. (2008). Neuronal mechanisms of visual stability. *Vision Research*, *48*(20), 2070–2089.

Figure Captions

Figure 1. Schematic representation of the four possible stimulus arrangements (for details, see

Mathôt & Theeuwes, 2010a). Participants execute two saccadic eye movements. The first

saccade (step 1) allowed us to dissociate retinotopic from spatiotopic coordinates. The latency of

the second saccade (step 2) was used as the measure of interest. The step 2 saccade target was

presented either at the same retinotopic location as the cue (actual retinotopic), the same spatial

location as the cue (actual spatiotopic), or one of two control locations (mirror retinotopic, mirror

spatiotopic). The interval between the offset of the cue, and the onset of the saccade target was

varied (stimulus onset asynchrony, SOA).

Figure 2. a) The effect of saccade latency on the strength of retinotopic and spatiotopic IOR

across all SOAs. For fast saccades, retinotopic IOR is stronger than spatiotopic IOR. For slow

saccades, spatiotopic IOR is stronger than retinotopic IOR. b) The effect of saccade latency and

SOA/ post-saccadic delay on retinotopic and spatiotopic IOR. The most prominent result is that

retinotopic IOR is largest for fast saccades in the shortest SOA (73ms post-saccadic delay),

whereas spatiotopic IOR is largest for slow saccades in the 1100ms SOA (634ms post-saccadic

delay). Error bars indicate within-subject standard errors (Cousineau, 2005). Shaded areas

indicate evidence for a difference between retinotopic and spatiotopic IOR (see text).

Retinotopic

Spatiotopic

Step 2

Step 1

Actual   Cue

Mirror

Actual

Mirror

a) Results across SOAs

b) Results per SOA