

# Remapping of the environment without corollary discharges: Evidence from scene-based IOR

**Shai Gabay\***

Department of Psychology, Carnegie Mellon University,  
Pittsburgh, PA, USA



**Yoni Pertzov\***

Department of Psychology, The Hebrew University of  
Jerusalem, Jerusalem, Israel



**Noga Cohen**

Department of Psychology and the  
Zlotowski Center for Neuroscience,  
Ben-Gurion University of the Negev, Beer-Sheva, Israel



**Galia Avidan**

Department of Psychology and the  
Zlotowski Center for Neuroscience,  
Ben-Gurion University of the Negev, Beer-Sheva, Israel



**Avishai Henik**

Department of Psychology and the  
Zlotowski Center for Neuroscience,  
Ben-Gurion University of the Negev, Beer-Sheva, Israel



Previous studies suggested that in order to perceive a stable image of the visual world despite constant eye movements, an efference copy of the oculomotor command is used to remap the representation of the environment in the brain. In two experiments, an inhibitory attentional component (inhibition of return—IOR) was used to examine whether remapping can occur also in the absence of eye movements. Participants were asked to maintain fixation while an unpredictable, attention-grabbing cue appeared and was then followed by a movement of the background image which was artificial (random dots, Experiment 1) or composed of natural scenes (Experiment 2). The participants were then required to respond to a target stimulus that was presented either at the same location as the cue relative to fixation (retinotopic), or at a matching location relative to the background (scene based). In both experiments, an IOR effect was found in scene-based locations immediately after the movement of the background. We suggest that remapping of the inhibitory tagging, which might be a proxy for remapping of the visual scene, could be accomplished rapidly even without the use of an efference copy; the inhibitory tag seems to be anchored to the background image and to move together with it.

## Introduction

The process of remapping space following the execution of eye movements has been the focus of research since the mid-twentieth century (Ross, Morrone, Goldberg, & Burr, 2001; Sperry, 1950). It has been suggested that the ability to maintain a stable perception of the surrounding visual world, despite the frequent execution of rapid eye movements, is achieved by using a copy of the motor command (Sommer & Wurtz, 2006). These internal signals (often termed corollary discharges) represent intended movement and were suggested to help in compensating for the retinal displacement resulting from eye movements (Sperry, 1950). This phenomenon is thought to be linked to particular neurons in the parietal cortex that shift their receptive field to a future location just prior to the execution of a saccade to that location (Duhamel, Colby, & Goldberg, 1992; Umeno & Goldberg, 1997). These neurons were also implicated in representing attentional priority as they exhibit stronger responses for behaviorally relevant items compared to distractors, even before the initiation of the saccade that brings the stimulus into the neurons' receptive field (Mirpour &

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Bisley, 2012). Interestingly, it was also demonstrated that previously attended targets produced reduced response than unattended targets, suggesting a probable link to the inhibition of return (IOR) phenomenon (see below for more details); but caution should be used when linking a neuronal response profile and response time effects (such as IOR).

Sommer and Wurtz (2006) elegantly demonstrated that this change in the receptive field of parietal neurons depends on inputs from corollary discharges arriving from the thalamus. This view implies that extra-retinal information about eye position and intended eye movements are involved in maintaining visual stability across eye movements.

In contrast to this view, Bays and Husain (2007) suggested that corollary discharges do not contribute to remapping of the environment but rather to action control, sensorimotor adaptation, and spatial memory. According to this account, maintaining a stable visual percept of the world following an eye movement would be achieved solely by visual cues that provide information about the location of objects in a world-based frame of reference.

A behavioral effect that may provide insight pertinent to this question is IOR (Posner & Cohen, 1984; Posner, Rafal, Choate, & Vaughan, 1985). This effect is typically observed during the Posner cuing task, which enables the examination of voluntary (endogenous) or reflexive (exogenous) orienting (for a review see Klein, 2000). When exogenous orienting is to be examined, as in the present study a nonpredictive peripheral cue is presented before a target stimulus that requires a response. The typical pattern of results is an early validity effect followed by IOR. That is, reaction time (RT) for valid trials (i.e., target and cue appear at the same location) is faster than for invalid trials (i.e., target and cue appear at opposite locations) at short cue-target intervals and slower for valid than for invalid trials at longer cue-target intervals.

In addition to the appearance of IOR in retinal coordinates, inhibitory tagging of IOR is also evident at the same position with relation to the head, body, or world (termed here collectively the *spatiotopic* position) following the execution of eye movements (Maylor & Hockey, 1985; Pertzov, Zohary, & Avidan, 2010; Sapir, Hayes, Henik, Danziger, & Rafal, 2004). Furthermore, a recent study generating a virtual parietal lesion in healthy controls by applying transcranial magnetic stimulation (TMS) showed that stimulation of the right (but not left) intraparietal sulcus abolished the spatiotopic IOR effect, but did not influence retinotopic IOR (van Koningsbruggen, Gabay, Sapir, Henik, & Rafal, 2010). These findings suggest that the right intraparietal sulcus is required for maintaining IOR at the same location in space in spite of egocentric movements. Since IOR was shown

to be anchored to a specific spatiotopic position following an eye movement, it can be used as a proxy for exploring the processes involved in maintaining visual stability following the execution of eye movements or movement of the world without any eye movements. If corollary discharges from the motor command are indeed essential for remapping of the visual surrounding, the absence of eye movements should lead to an IOR effect that will be evident only at the retinal location and will not be updated as a result of background movement. That is, if IOR is observed in the same location relative to the background following its movement, we could conclude that retinal cues are sufficient to update the inhibitory tagging generated by peripheral stimuli. This finding would suggest that extra-retinal information (i.e., efference copy) is not necessary for maintaining visual stability.

It was previously demonstrated that IOR could be associated with dynamic, object-based representations (Becker & Egeth, 2000; Tipper, Driver, & Weaver, 1991); yet, eye movements were not controlled in these experiments. Hence, it is not clear whether IOR was apparent at the cued object as a result of a change in eye position, or as a result of remapping of the environment. It was also suggested that object-centered and environment-centered orienting of attention are related to different brain structures (Wilson, Woldorff, & Mangun, 2005). Recently, Krüger and Hunt (2013) demonstrated that IOR was evident in both retinotopic and spatiotopic locations following an eye movement. Yet IOR was not observed at the updated cued location when the set of possible locations moved together with a background frame (without performing any eye movements). The authors concluded that an efference copy plays a key role in maintaining inhibition of previously attended objects across saccades. Note that in Krüger and Hunt's (2013) study, the effect of IOR was examined 500 ms following the shift in the image. Previous studies have demonstrated that the spatiotopic IOR effect is most pronounced immediately after the visual movement (Hilchey, Klein, Satel, & Wang, 2012; Pertzov et al., 2010). It is possible that in the 500 ms that passed following the shift of the image, IOR was already abolished. Another possible factor that could have influenced Krüger and Hunt's (2013) results was the usage of a rapid visual shift in the image, instead of using a more gradual motion pattern that would have enhanced the perception of a continuous unitary visual display rather than two separate visual displays. In addition, in contrast to object-based effects, remapping of the visual scene should be more critical for scene-based IOR, in which there is no distinct object representation that can be "tagged" with inhibition.

## The current study

Here, in two experiments we examine how movement of a background image in the absence of eye movements influences IOR. This is in contrast to previous work examining scene-based IOR following execution of eye movements. If the oculomotor command is indeed essential for remapping inhibitory tagging, we expect to find IOR only at the retinal coordinates, rather than at the remapped location according to the movement of the background.

As indicated earlier, IOR can be tagged to objects even if they move in space (Becker & Egeth, 2000). However, importantly, in those past studies an object was cued and IOR was measured for targets appearing inside that object, a condition which prevented the dissociation between object-based and spatial attention effects. In contrast, in the present study we wish to examine a different question, that is, whether IOR is coded purely in scene-based coordinates, without the involvement of a clear bounded object. Therefore, the inhibited location was not marked by spatial landmarks (e.g., place holders) to indicate the possible target locations as was commonly done in previous cuing tasks. In the first experiment, in which we used artificial background images, we also made sure that these images would not be composed of any stimuli presented close to the possible target locations. Thus, in the present experimental design, the inhibitory tagging could only be remapped if it was attached to the visual background itself (for an illustration of the experimental design, see Figure 1A). To simulate the influence of eye movements on the retinotopic image, the visual scene in our task moved in a specific direction (i.e., on one edge of the image the background figure disappeared while on the opposite edge a new part appeared), yet the cued location (relative to the background movement) remained visible throughout the trial. The second experiment was similar, but here natural scenes were used as background images in order to make the experiment more ecologically valid.

## Experiment 1

### Methods

#### Participants

Fifteen participants, all first year psychology students from Ben-Gurion University of the Negev, participated in the experiment in return for course credit. All participants had normal or corrected-to-normal vision by self-report. The experiment was

approved by the ethics committee of the Psychology Department.

#### Apparatus and stimuli

Stimuli were displayed on a 19 in. CRT monitor (Graphics Series G90fB; View Sonic) at a resolution of  $1024 \times 768$  pixels, with a refresh rate of 60 Hz. The stimuli were presented on a black background and consisted of a fixation cross (which subtended a visual angle of  $1^\circ$ ) at the center of the computer screen, and 20 white dots (each  $1.5^\circ$  in diameter). Four different background images were created. The 20 dots of the background images were distributed randomly with the restriction they could not be located around the four possible cued locations before, during, or following the background displacement. In each trial a red target circle ( $0.5^\circ$ ) appeared in one of the corners of an invisible  $8^\circ$  square, centered at the fixation cross. The appearance of the target circle was preceded by a brief presentation of a white square (i.e., the cue) for 100 ms and a movement of the background dots for 100 ms,  $8^\circ$  (at a speed of  $80^\circ/s$ ) to one of the four cardinal directions (up, down, left, or right). A video-based desktop-mounted eye tracker (Eye Link1000, SR Research, Ontario, Canada) with a sampling rate of 1000 Hz was used for recording eye movements. We used built-in programs provided with the eye tracker for calibration and validation purposes (9 points presented in a random sequence). All the data analyzed in the present study were obtained from recordings with an average Cartesian prediction error of less than  $1^\circ$  during the validation procedures.

#### Procedure

Participants were tested in a dark room with ambient light omitted by the eye-tracking equipment. They were seated 57 cm in front of the computer monitor and were instructed to maintain fixation on the fixation cross throughout the experiment and to avoid blinking during the trials (and blink only between trials). An on-line process verified whether their gaze shifted more than  $1.5^\circ$  away from fixation, in which case, an error sound was played and the trial was aborted and presented again later in the experiment. Participants were instructed to press the left button of a mouse as fast as possible when the target circle appeared, but to avoid false responses. Participants were also informed that the peripheral cue was not informative as to where the target would appear. Trials were self-paced and began with the participant pressing the space bar while fixating the central fixation, which initiated a drift correction process and allowed time for blinks. The visual presentation consisted of the center display of the background image (an additional  $8^\circ$  of the

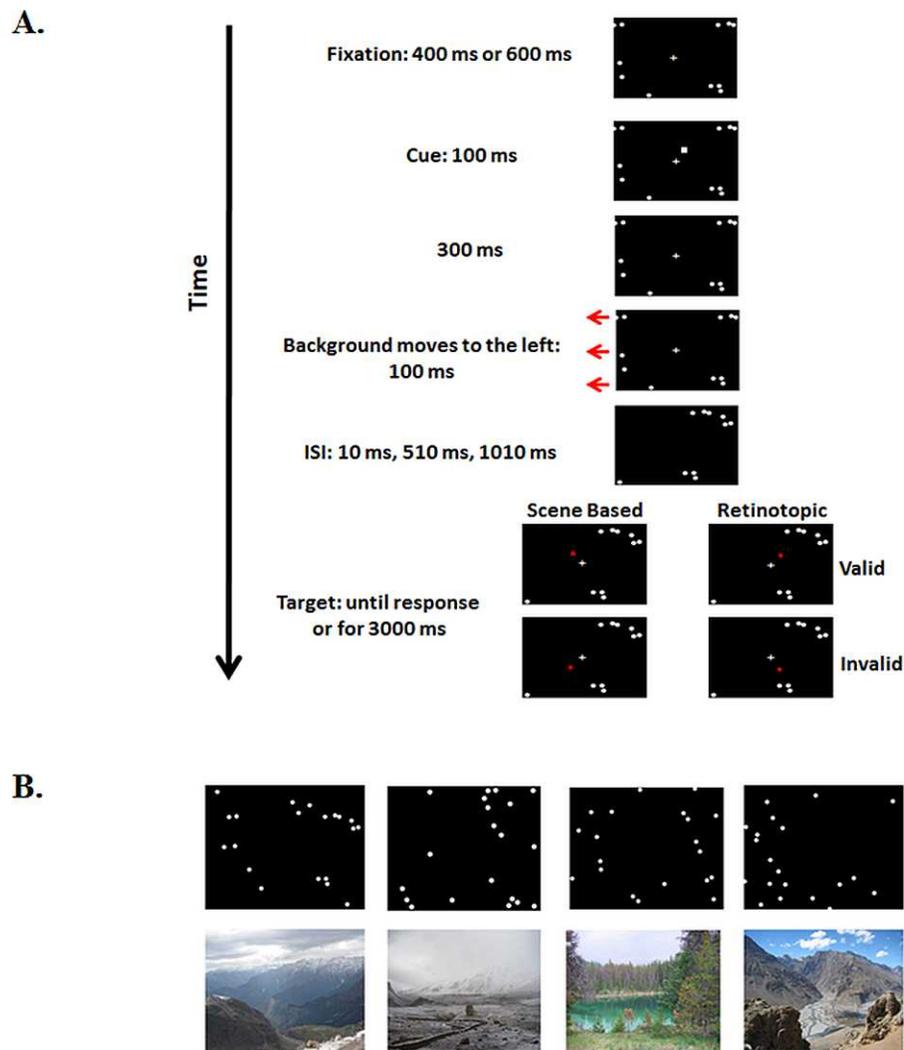


Figure 1. (A) Experimental design with four possible target locations (shown with an example of a background image taken from Experiment 1). After the presentation of an un-predictive cue (white square), the background image shifted  $8^\circ$  in one of the four cardinal directions (left, right, up, or down). Then, a target (red circle) appeared at one of four possible locations corresponding to the four different conditions: Scene-based valid, scene-based invalid, retinotopic valid, and retinotopic invalid. (B) The four background images used in Experiment 1 (top row) and Experiment 2 (bottom row).

background image was maintained on each side of the display, in order to allow the movement of the background without introducing any blank background at the edges) and a fixation cross, which was present throughout the experiment. Four hundred or 600 ms after the beginning of a trial, a white square cue was presented for 100 ms in one of the four corners of an  $8^\circ$  invisible square that was centered on the fixation cross. Three hundred ms after the offset of the cue, the background dots moved  $8^\circ$  to one of two directions, depending on the cue location. The background dots only moved in an opposite direction from the cued location. That is, for a trial in which the cue appeared at an upper-right location, background dots could move either down or left (not up or right). The

background dots moved for 100 ms, after which there was an ISI (interstimulus interval) of 10 ms, 510 ms, or 1010 ms. IOR was expected to be found at all ISIs since the cue-target interval was longer than 300 ms (see Klein, 2000), allowing sufficient time for IOR to develop.

Following the ISI, the target circle appeared in one of the corners of the  $8^\circ$  square that was centered at the fixation cross. In valid trials, the target circle could appear at the scene location (the location at which the target appeared relative to the background but now both displaced by the  $8^\circ$  background shift) or at the retinotopic location (relative to fixation). In invalid trials, the target circle appeared opposite to the scene-based location relative to the background movement.

For example, if the background moved horizontally and the cue appeared above fixation, the invalid locations would be below fixation. If the background moved vertically and the cue appeared to the left of the fixation, the invalid locations would be on the right of fixation (see Figure 1). The target remained visible until the participant responded, by pressing a mouse button, or for a maximum of 3000 ms. There were 32 catch trials in which no target appeared and participants were required not to respond, and there were 32 practice trials before the experiment began. The experiment contained a total of 416 trials (divided into four blocks) in which 192 were valid and 192 were invalid trials (32 trials for every validity condition and SOA condition).

There were no trials in which the participants' response was very slow ( $\geq 1500$  ms). Trials in which participants performed eye movements or blinked were aborted and presented again at a later stage during the task (accounting for 17% of the trials). Participants did not make false responses during catch trials.

## Results

Median RT, as a function of target coordinate type, validity, and ISI are presented in Figure 2. Median RTs were used to reduce susceptibility to outlier RTs. It should be noted that the ISI is the time from the end of the background movement until target presentation. The duration between cue presentations and target appearance, which is commonly reported in similar attention tasks, is 500 ms longer than the ISI. Based on previous studies, IOR is expected after 300 ms from cue presentation (see Klein, 2000); thus, it is expected to appear in all ISIs used in the present task. Analysis of variance (ANOVA) with ISI (10 ms, 510 ms, 1010 ms), coordinate type (scene-based, retinotopic), and validity (valid, invalid) on participants' median RTs revealed a significant main effect of ISI,  $F(2, 28) = 62.4$ ,  $p < 0.001$ , which was due to longer RT at the first interval compared to the later intervals. This effect is termed the fore period effect (Näätänen, 1970) and is often attributed to expectation effects that are observed in experimental designs that use different ISIs. The main effect of validity was also significant,  $F(1, 14) = 9.7$ ,  $p < 0.01$ , due to faster RT for invalid than for valid targets (IOR). The main effect of coordinate type was also significant,  $F(1, 14) = 16.8$ ,  $p < 0.01$ , RT for scene-based coordinates was faster than for retinal coordinates. Finally, the three-way interaction was also significant,  $F(2, 28) = 4.7$ ,  $p < 0.05$ . We continued to examine this interaction by exploring the time course of IOR for every coordinate type separately. For the scene-based coordinate type, IOR was significant at the first ISI,  $F(1, 14) = 19.7$ ,  $p < 0.001$ ;  $F(1, 14) < 1$ ,  $ns$ ;  $F(1, 14) < 1$ ,  $ns$ ; for 10 ms, 510 ms, and 1010 ms ISIs,

respectively. For the retinotopic coordinate type, IOR was significant at the last ISI,  $F(1, 14) < 1$ ,  $ns$ ;  $F(1, 14) = 1.3$ ,  $ns$ ;  $F(1, 14) = 12.1$ ,  $p < 0.01$ ; for 10 ms, 510 ms, and 1010 ms ISIs, respectively.

We can conclude that both scene-based and retinotopic locations demonstrated IOR with different dynamics. IOR at the scene-based location was evident very early after the background movement while retinotopic IOR was presented only at a later stage.

## Discussion

In this experiment we demonstrated that IOR is present at scene-based and retinotopic coordinates even when eye movements, and hence oculomotor commands, were not executed. This finding strengthens the claim that oculomotor commands are not essential for remapping inhibitory tagging.

Interestingly, while we documented IOR for both scene-based and retinotopic IOR, the two forms of IOR exhibited different dynamics. While scene-based IOR appeared immediately after the movement of a background image and decayed rapidly, retinal IOR evolved as time elapsed and was only evident at the latest ISI. The appearance of scene-based IOR very early after the movement of the background image suggests that remapping of the environment can be accomplished by visual cues (retinal) that provide information regarding the spatial coordinates of the visual world. This finding can also explain the lack of object-based IOR in a study by Krüger and Hunt (2013) that examined the presence of IOR only 500 ms after an object shift.

Notably, rapid formation of IOR in a scene-based frame of reference was previously demonstrated in a task measuring retinotopic and spatiotopic IOR following eye movements (Pertzov et al., 2010). Several studies support the suggestion that retinal and spatiotopic IOR may be related to, at least partly, distinct neural mechanisms. Thus, for example, a study by Sapir, Soroker, Berger, and Henik (1999) implies that the superior colliculus is involved in the generation and presentation of both retinotopic and scene-based IOR, while other studies have demonstrated the involvement of parietal regions in scene-based, but not retinotopic IOR (Sapir et al., 2004; van Koningsbruggen et al., 2010). Regardless of the exact neural mechanism related to each form of IOR, the inhibitory tagging assigned to the specific location in a scene-based frame of reference prior to the appearance of IOR in retinal coordinates could be viewed as supportive evidence for functional independence of these two processes. Moreover, this finding reinforces the claim that scene-based IOR does not depend exclusively on extraretinal information.

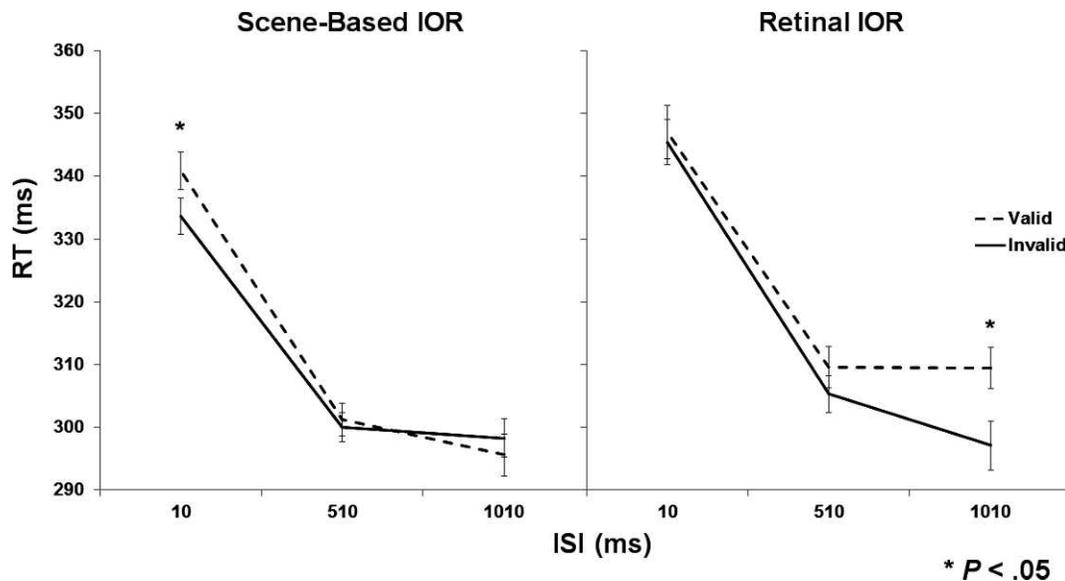


Figure 2. Results of Experiment 1: Median RT as a function of target coordinates, validity, and ISI. As can be seen, participants presented an early scene-based inhibitory component and a late retinotopic inhibitory component. The ISI presented in the graphs relates to the time following background movement and the appearance of the target. Error bars represent standard error of the mean adjusted to a within-subject design (Cousineau, 2005).

The finding that RT for scene-based coordinates was faster than that for retinal coordinates might have influenced the pattern of results and, hence, confounded our findings. This difference might be related to the usage of artificial background images. It is possible that these images enhanced the perception of motion and facilitated the remapping of the attentional effects at this location, including the formation of IOR in the scene-based reference frame. It is also possible that these stimuli were not perceived in the same way as natural scenes would have been processed, and this distinction might have biased our findings. To address these issues, in the next experiment we used more ecological background images rather than the artificial ones used in Experiment 1 (see Figure 1B). All other experimental procedures were identical.

## Experiment 2

### Methods

#### Participants

Fifteen participants (none of whom participated in Experiment 1), performed the experiment in return for payment. All participants had normal or corrected-to-normal vision by self-report. The experiment was approved by the ethics committee of the Psychology Department.

#### Apparatus and stimuli

The design and apparatus were identical to those of Experiment 1 except for the replacement of the background images (see Figure 1B; the images used were photographs taken by one of the authors).

#### Procedure

The procedure was identical to that of the first experiment. Trials in which the participants responded very slow ( $\geq 1500$  ms, less than one percent of the data) were excluded from the analysis. In 30% of the trials an eye movement or blink was detected by the on-line eye-tracking process, and these trials were aborted and presented again at a later stage during the task. The appearance of more eye movements in this experiment, leading to a greater percentage of aborted trials compared to the first experiment (30% vs. 17%, respectively), might have been a result of the difference in the background images. Real-world background images are more cluttered, especially around fixation, and therefore are more likely to generate smooth pursuit eye movements that follow the background movement. Participants did not make any false responses during catch trials.

### Results

Median RT as a function of target coordinate, validity, and ISI are presented in Figure 3. An

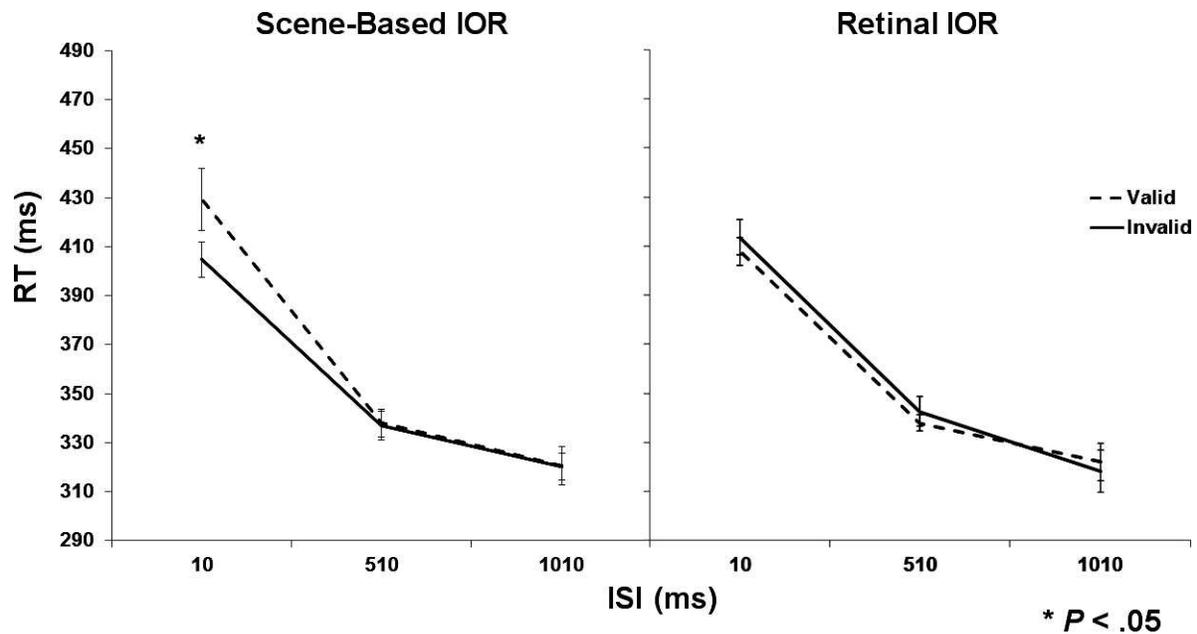


Figure 3. Results of Experiment 2: Median RT as a function of target coordinates, validity, and ISI. As can be seen, participants presented an early, scene-based inhibitory component but no retinotopic inhibitory component. Error bars are calculated as in Figure 2.

ANOVA with ISI (10 ms, 510 ms, 1010 ms), coordinate type (scene-based, retinotopic) and validity (valid, invalid) on participants' median RTs revealed a significant main effect of ISI,  $F(2, 28) = 44.6$ ,  $p < 0.001$ , which was due to longer RT at the first interval compared to the later intervals. As in the first experiment, the three-way interaction was also significant,  $F(2, 28) = 4.1$ ,  $p < 0.05$ . We continued to examine this interaction by exploring the time course of IOR for every coordinate type separately. For the scene-based coordinate type, IOR was significant at the first ISI,  $F(1, 14) = 11.2$ ,  $p < 0.01$ ;  $F(1, 14) < 1$ ,  $ns$ ;  $F(1, 14) < 1$ ,  $ns$ ; for 10 ms, 510 ms, and 1010 ms ISIs, respectively. For the retinotopic coordinate type, IOR was not significant at any ISI,  $F(1, 14) = 1$ ,  $ns$ ;  $F(1, 14) < 1$ ,  $ns$ ;  $F(1, 14) < 1$ ,  $ns$ ,  $p < 0.01$ ; for 10 ms, 510 ms, and 1010 ms ISIs, respectively.

As in the first experiment, the scene-based location experimental condition demonstrated IOR, which was evident very early after the background movement. Retinotopic IOR was not detected at any SOA.

## Discussion

In the second experiment we replicated the finding that IOR can be remapped after a movement of the background even without eye movements. In this experiment we used a set of ecological background images in order to examine this phenomenon in a more naturalistic setting compared to that of Experiment 1.

Using this design, we were able to replicate our main finding: an early IOR at spatiotopic coordinates. In contrast, IOR was not observed at the retinal coordinates at any of the ISIs. It has been previously demonstrated that the level of cue processing can modulate IOR (Gabay, Chica, Charras, Funes, & Henik, 2012); thus, this discrepancy between the results of the two experiments might result from a masking influence on cue processing by the natural images' saliency and consequently, its processing is reduced, leading to a smaller, delayed, IOR effect. It is possible that a wider range of ISIs is necessary for detecting the presence of IOR in this setting. Note, however, that this presumed reduction in cue processing did not influence IOR at the scene-based location. Possibly the more ecological background images also facilitated the updating of the inhibitory process following scene movement, which preserved IOR magnitude at that location.

## General discussion

In two separate experiments we demonstrated the presence of IOR in scene-based coordinates immediately following movement of a background scene without the execution of eye-movements.

It is widely accepted that in order to perceive a stable image of the visual world despite constant eye movements, an efference copy of the oculomotor

command is utilized to remap the representation of the environment in the brain (Sommer & Wurtz, 2006). Here, using an inhibitory attentional component (the IOR effect), we challenged this account and asked whether remapping of internal representations can also occur in the absence of eye movements. Our key finding is that remapping of IOR for scene-based locations, following movement of the background image, can occur even without the execution of eye movements. Consequently, we suggest that remapping of the environment might not be completely dependent on corollary discharges.

The ability to perceive a stable world in the presence of rapid, ballistic eye movements has been the focus of a long-standing debate. One approach emphasizes the importance of extraretinal information, such as corollary discharges, in maintaining the perception of a stable image of the world (Duhamel et al., 1992; Sommer & Wurtz, 2006). An intuitive support for this account comes from the simple demonstration that eye movements not generated by volitional eye muscle activity (such as a fingertip pressing against the eyeball) produce the sensation of external motion. Additional, more rigorous support comes from the finding, mentioned earlier, that neurons in the parietal cortex shift their receptive field to a future location *prior* to the execution of a saccade (Duhamel et al., 1992; Umeno & Goldberg, 1997). These findings provided the basis for a wide consensus regarding the importance of corollary discharges in maintaining the perception of a stable world during and after saccades (for a review see Ross et al., 2001). An alternative account, however, suggests that corollary discharges may not have a major role in remapping of the environment following saccades. For example, Bays and Husain (2007) claimed that corollary discharges may be involved only in non-perceptual processes such as action control, sensorimotor adaptation, and spatial memory. This view is supported by the finding that participants' ability to detect object displacement during a saccade depends on the relative locations between the presented objects rather than their absolute retinal positions (Carlson-Radvansky & Irwin, 1995; Deubel, 2004; Germeys, De Graaf, Panis, van Eccelpoel, & Verfaillie, 2004). Our work is in accordance with this latter view: We demonstrated that an attentional effect (IOR) can be remapped following a change in the background image, even without feedback of corollary discharges, normally resulting from the execution of a saccade.

It should be noted that the ability to remap the inhibitory tagging using only visual cues, without performing eye movements, does not refute the possibility that during saccades other processes are also involved in maintaining stable internal representations of the environment. It is possible that additional

processes are involved in maintaining stable percept of the world. Yet, our finding indicates that such environmental updating can occur even without the involvement of corollary discharges. This finding, in turn, weakens the suggestion that extra-retinal information is indispensable for remapping of the visual world.

It was previously demonstrated that IOR could be tagged to dynamic, object-based representations (Tipper et al., 1991). The present work is, to the best of our knowledge, the first, to demonstrate remapping of IOR in scene-based coordinates without being tagged to a specific object and without eye movements. Our work shows that an inhibitory component can be mapped based on an environmental coordinate frame alone.

It should be noted that in addition to the notion of being a perceptual phenomenon, IOR was also suggested to be a motor effect that inhibits the motor/ocular motor responses to the cued location/object. This view of the IOR weakens the direct link between remapping of IOR and maintaining visual stability. Even if IOR is purely a motor process, the remapping of the motor plan following the movement of the background image must have relied on some computations that had to have happened without the presence of corollary discharges (since no eye movements occurred). Another possibility that should be considered is that the mechanisms involved in shifting IOR during passive viewing of a scene in motion may not be identical to those used when shifting across a saccade. For instance, it is possible that when the visual display moves at relatively high velocity (as in our task), an automatic shifting of spatial processing might occur (similar to the automatic processes guiding smooth eye pursuit), but this shift might not necessarily occur at different velocities of background movement. Future work should examine the sensitivity of scene-based IOR to various types of background movements.

Critically, single cell recordings in monkeys have shown that attentional shifts, which are not accompanied by eye movements, do not produce neural remapped visual response at the lateral intraparietal area as when a saccade is performed (Colby, 1996). Hence, attentional shifts alone are not likely to account for the present findings (for a review see Berman & Colby, 2009). The lack of eye movements in our task, and hence the lack of corollary discharges, suggests that visual information is a key factor in remapping of IOR. This shift in turn, provides a possible indication for the claim that corollary discharges are not necessary for remapping of the visual scene and visual stability (Bays & Husain, 2007).

*Keywords: remapping of the environment, efference copy, inhibitory tagging, eye movements*

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\* SG and YP contributed equally to this article.

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Corresponding author: Shai Gabay.

Email: shaigaba@gmail.com.

Address: Department of Psychology, Carnegie Mellon University, Pittsburgh, PA, USA.

## References

- Bays, P. M., & Husain, M. (2007). Spatial remapping of the visual world across saccades. *NeuroReport*, *18*, 1207–1213.
- Becker, L., & Egeth, H. (2000). Mixed reference frames for dynamic inhibition of return. *Journal of Experimental Psychology: Human Perception and Performance*, *26*, 1167–1177.
- Berman, R., & Colby, C. (2009). Attention and active vision. *Vision Research*, *49*, 1233–1248.
- Carlson-Radvansky, L. A., & Irwin, D. E. (1995). Memory for structural information across eye movements. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *21*, 1441–1458.
- Colby, C. L. (1996). A neurophysiological distinction between attention and intention. In J. McClelland & T. Inui (Eds.), *Attention and performance XVI: Information integration in perception and communication* (pp. 157–177). Cambridge, MA: M.I.T. Press.
- Cousineau, D. (2005). Confidence intervals in within-subject designs: A simpler solution to Loftus and Masson's method. *Tutorial in Quantitative Methods for Psychology*, *1*(1), 42–45.
- Deubel, H. (2004). Localization of targets across saccades: Role of landmark objects. *Visual Cognition*, *11*, 173–202.
- Duhamel, J. R., Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science*, *255*, 90–92.
- Gabay, S., Chica, A. B., Charras, P., Funes, M. J., & Henik, A. (2012). Cue and target processing modulate the onset of inhibition of return. *Journal of Experimental Psychology: Human Perception and Performance*, *38*, 42–52.
- Germeys, F., De Graaf, P., Panis, S., van Eccelpoel, C., & Verfaillie, K. (2004). Transsaccadic integration of bystander locations. *Visual Cognition*, *11*, 203–234.
- Hilchey, M. D., Klein, R. M., Satel, J., & Wang, Z. (2012). Oculomotor inhibition of return: How soon is it “recoded” into spatiotopic coordinates? *Attention, Perception & Psychophysics*, *74*, 1145–1153.
- Klein, R. (2000). Inhibition of return. *Trends in Cognitive Sciences*, *4*, 138–146.
- Krüger, H. M., & Hunt, A. R. (2013). Inhibition of return across eye and object movements: The role of prediction. *Journal of Experimental Psychology: Human Perception and Performance*, *39*, 735–744.
- Maylor, E. A., & Hockey, R. (1985). Inhibitory component of externally controlled covert orienting in visual space. *Journal of Experimental Psychology: Human Perception and Performance*, *11*, 777–787.
- Mirpour, K., & Bisley, J. W. (2012). Anticipatory remapping of attentional priority across the entire visual field. *Journal of Neuroscience*, *32*, 16449–16457.
- Näätänen, R. (1970). The diminishing time-uncertainty with the lapse of time after the warning signal in reaction-time experiments with varying fore-periods. *Acta Psychologica*, *34*, 399–419.
- Pertsov, Y., Zohary, E., & Avidan, G. (2010). Rapid formation of spatiotopic representations as revealed by inhibition of return. *Journal of Neuroscience*, *30*, 8882–8887.
- Posner, M. I., & Cohen, Y. P. C. (1984). Components of visual orienting. In H. Bouma & D. Bouwhuis (Eds.), *Attention and performance X* (pp. 531–556). London, England: Erlbaum.
- Posner, M. I., Rafal, R. D., Choate, L. S., & Vaughan, J. (1985). Inhibition of return: Neural basis and function. *Cognitive Neuropsychology*, *2*, 211–228.
- Ross, J., Morrone, M. C., Goldberg, M. E., & Burr, D. C. (2001). Changes in visual perception at the time of saccades. *Trends in Neurosciences*, *24*, 113–121.
- Sapir, A., Hayes, A., Henik, A., Danziger, S., & Rafal, R. (2004). Parietal lobe lesions disrupt saccadic remapping of inhibitory location tagging. *Journal of Cognitive Neuroscience*, *16*, 503–509.
- Sapir, A., Soroker, N., Berger, A., & Henik, A. (1999). Inhibition of return in spatial attention: Direct evidence for collicular generation. *Nature Neuroscience*, *2*, 1053–1054.
- Sommer, M. A., & Wurtz, R. H. (2006). Influence of the thalamus on spatial visual processing in frontal cortex. *Nature*, *444*, 374–377.
- Sperry, R. W. (1950). Neural basis of spontaneous

- optokinetic responses produced by visual inversion. *Journal of Comparative and Physiological Psychology*, *43*, 482–489.
- Tipper, S. P., Driver, J., & Weaver, B. (1991). Object-centered inhibition of return of visual attention. *Quarterly Journal of Experimental Psychology*, *43*, 289–298.
- Umeno, M. M., & Goldberg, M. E. (1997). Spatial processing in the monkey frontal eye field. I. Predictive visual responses. *Journal of Neurophysiology*, *78*, 1373–1383.
- van Koningsbruggen, M. G., Gabay, S., Sapir, A., Henik, A., & Rafal, R. D. (2010). Hemispheric asymmetry in the remapping and maintenance of visual saliency maps: A TMS study. *Journal of Cognitive Neuroscience*, *22*, 1730–1738.
- Wilson, K. D., Woldorff, M. G., & Mangun, G. R. (2005). Control networks and hemispheric asymmetries in parietal cortex during attentional orienting in different spatial reference frames. *NeuroImage*, *25*, 668–683.