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Updating visual–spatial working memory during object movement



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ABSTRACT

Working memory enables temporary maintenance and manipulation of information for immediate access by cognitive processes. The present study investigates how spatial information stored in working memory is updated during object movement. Participants had to remember a particular location on an object which, after a retention interval, started to move. The question was whether the memorized location was updated with the movement of the object or whether after object movement it remained represented in retinotopic coordinates. We used saccade trajectories to examine how memorized locations were represented. The results showed that immediately after the object stopped moving, there was both a retinotopic and an object-centered representation. However, 200 ms later, the activity at the retinotopic location decayed, making the memory representation fully object-centered. Our results suggest that memorized locations are updated from retinotopic to object-centered coordinates during, or shortly after object movement.

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1. Introduction

Imagine waving goodbye to a friend as his train is leaving the station. Due to the reflection in the windows and objects blocking the view you might not be able to constantly see him. Still, even when the train starts to move you are perfectly able to keep track of his location within the train and you know where to wave at. In this process, our spatial working memory plays a crucial role. It allows us to temporarily maintain and manipulate information about locations of objects around us. This ability preserves the coherency of information processing when the objects of interest disappear from our view. Although successful interaction with our environment requires information about the world-centered location of objects, empirical evidence shows that spatial information is most likely stored in a retinotopic coordinate system (Duhamel, Colby, & Goldberg, 1992; Golomb, Chun, & Mazer, 2008; Golomb & Kanwisher, 2012). This poses significant challenges to the operation of the spatial memory system; with every intervening eye-, body- or object movement the locations of interest change their position on the retina. To compensate for these displacements, retinotopic representations have to be updated constantly. Recent evidence shows that when making a saccade, attended or memorized locations are gradually remapped from retinotopic to spatiotopic coordinates (Golomb, Chun, & Mazer, 2008; Mathot & Theeuwes, 2010; Rolfs et al., 2011). Feedback from the oculomotor system about

upcoming eye movement is thought to be of crucial importance for this process (Sommer & Wurtz, 2008). However, such signals are not available when only the objects of interest are moving.

Previous studies have demonstrated that attention can operate in object-centered coordinates. For example, exogenous attention has been shown to travel with a moving object. Depending on the time-course it produced either object-centered facilitation (Boi et al., 2011; Theeuwes, Mathot, & Grainger, 2013; Umiltà et al., 1995) or object-centered inhibition of return (Tipper, Brehaut, & Driver, 1990; Tipper, Driver, & Weaver, 1991; Tipper et al., 1994). In addition, it has been shown that visual neglect, a neuropsychological condition commonly associated with ignoring one side of the visual field, can also be manifested in object-based fashion. Specifically, patients have been shown to ignore one side of an object, independently of location of the object in visual space (Tipper & Behrmann, 1996). Furthermore, single-cell recordings in monkeys have revealed object-based selectivity of neurons in the supplementary eye fields (Olson, 2001, 2003; Olson & Gettner, 1996; Tremblay, Gettner, & Olson, 2002). For example, some neurons fired only if a particular side of an object was kept in memory, independently of the retinal location of the object (Olson, 2003). While many studies have shown that attention can reside in object-centered coordinates, the mechanisms of creating and updating these object-based representations remain largely unclear.

The present study investigated how spatial working memory is updated during object movement. Subjects had to memorize a location on an object which, after a retention interval, started to move. At different times after object movement a saccade had to be executed which trajectory either could go along the original retinotopic location or along the updated object-centered location.

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It has been shown that the maintenance of a location in working memory causes eyes to curve away from that location (Belopolsky & Theeuwes, 2011; Theeuwes, Olivers, & Chizk, 2005), just like the eyes curve away from attended objects in the real world (Doyle & Walker, 2001; Godijn & Theeuwes, 2002; Sheliga, Riggio, & Rizzolatti, 1994). This saccade curvature is thought to be a consequence of the preparation and subsequent inhibition of an eye movement to the memorized location (Doyle & Walker, 2001; Sheliga, Riggio, & Rizzolatti, 1995). Here the curvature was used to investigate how a memorized location is represented at different times after object movement. The question was whether the memorized location was updated with the movement of the object or whether it was still represented in retinotopic coordinates after the movement was completed.

2. Material and methods

Programming of the experiment was done using OpenSesame version 0.25 (Mathot, Schreij, & Theeuwes, 2011). The stimuli were presented on a 21 in. monitor running at 100 Hz with a 1024×768 pixel resolution. Eye movements were recorded with the EyeLink 1000 (SR Research) at a temporal resolution of 1 kHz.

A total of 21 volunteers (15 females), aged between 18 and 28, took part in a 75 min experiment consisting of a practice session followed by 256 experimental trials. They were seated at a distance of 75 cm from the computer screen with head positioned on a chinrest. A grey rectangular object with a width of 18.75 degrees of visual angle ($^{\circ}$) and a height of 12.5° (luminance: 44 cd/m^2) was presented in the middle of the screen. To increase the contrast with the black background the edges were colored white. In the center of the screen a red fixation cross was shown. After fixating this point for 2000 ms a white memory cue was flashed for 500 ms in one of the four quadrants of the object (equally likely in the left and right hemifield). The position was randomly selected out of 9 possible locations in this quadrant; at a horizontal distance of 1.9° , 2.8° , or 3.7° and a vertical distance of 2.2° , 2.5° , or 2.8° from the center of the screen.

After a retention interval between 1000 and 3000 ms the object could equally likely move upwards or downwards, covering a distance between 4.4° and 5.6° . If the memory cue was presented in one of the top quadrants the object was subsequently shifted downwards. If the memory cue had been presented in one of the bottom quadrants the object would move upwards. While participants could potentially predict the direction of object movement from the cue location, the variable amplitude of the object movement caused the exact updated location of the cue to be unpredictable. Four different frames were shown in succession during 150 ms. This was perceived as a smooth movement. Participants had to update the cue position in memory as the object moved, while keeping their eyes on the fixation cross. After the object stopped moving the fixation cross jumped 9.4° either directly above or below the center of the screen and participants had to make a saccade to it as fast as possible. In half of the trials object movement and eye movement were made in the same direction, so that the eyes moved into the same hemifield as the updated object-centered location. In the other half of the trials object movement and eye movement were in the opposite directions, so that the eyes moved into the same hemifield as the original retinotopic location of the memory cue (see Fig. 1). Importantly, to measure the time-course of the memory updating, on some trials a saccade had to be made directly following the object movement, while on the other trials there was a delay of 200 ms before the saccade target was presented. If saccade was made too early participants heard a tone. After saccade was detected all the stimuli remained on the screen for another 400 ms after which they were replaced

by a mask consisting of a random pattern of grey and black squares having a base of 2.7° . This was done in order to encourage participants to actively maintain and update the cue location in memory, instead of relying on landmarks. After another 1000 ms a mouse cursor appeared, and participants were instructed to click on the location on the screen where the memorized location was situated after the object movement.

To determine the effect of the memorized location on saccade trajectory, we calculated the angular deviation of the saccade path for each 1-ms sample point that was further than 0.5° from the central fixation and further than 0.5° from the endpoint of the saccade, relative to a straight line from the starting point of the saccade to the saccade endpoint. A median of these deviations was calculated for each saccade, averaged across saccade direction and normalized to the upper hemifield (curvature for memorized location on the left minus curvature for memorized location on the right, for a similar method see Godijn & Theeuwes, 2004; Van der Stigchel, Meeter, & Theeuwes, 2006).

3. Results

Four participants were excluded from the analysis because, despite extensive training, they were unable to give an accurate indication of the correct (object-centered) location (within 2.5°) in at least 50% of the trials. Trials in which a saccade was made before the saccade target appeared were excluded from further analysis. In addition, trials with saccades faster than 80 ms and slower than 600 ms, saccades that did not start within 1° away from the fixation point, saccades that were smaller than 3° , and saccades that did not land within 30° of arc from the saccade target were discarded. This resulted in the average loss of 12.1% of all trials.

There was a significant difference ($t(16) = 8.39$, $p < 0.001$) between the saccadic latencies for the short SOA (217 ms) and long SOA (192 ms). This means that the actual time between the end of the object movement and the onset of the saccade was 217 ms for the short SOA and 392 ms ($200 + 192$ ms) for the long SOA. Mean saccade curvature away in the retinotopic and object-centered conditions is presented in Fig. 2. The average saccade trajectories are plotted in Fig. 3. A repeated measures ANOVA with SOA (0 ms or 200 ms) and condition (retinotopic or object-centered) as factors revealed no main effect of either SOA ($F(1,16) = 1.78$; $p = 0.20$) or condition ($F(1,16) = 0.23$; $p = 0.64$). However, there was a significant interaction between SOA and condition ($F(1,16) = 5.97$; $p = 0.03$), indicating a different time-course of curvature away in the two conditions. Post hoc analysis revealed that over time curvature away from the retinotopic location significantly decreased (two-tailed t -test: $t(16) = 2.21$; $p = 0.04$), but for the object-centered location the curvature did not change significantly (two-tailed t -test: $t(16) = 0.64$; $p = 0.53$).

Further analysis showed that curvature away from the retinotopic location of the memory cue was significantly different from zero if a saccade was made directly after the object movement (0.87° ; one-tailed t -test: $t(16) = 3.90$; $p < 0.001$). However, there was no significant curvature away from the retinotopic location for the long SOA (0.14° ; one-tailed t -test: $t(16) = 0.74$; $p = 0.24$). Curvature away from the object-centered location was significantly different from zero for both short (0.36° ; one-tailed t -test: $t(16) = 2.46$; $p = 0.01$) and long SOAs (0.51° ; one-tailed t -test: $t(16) = 2.84$; $p < 0.01$). Direct comparison between conditions showed that for the short SOA the eyes curved away marginally more from the retinotopic location than from the object-centered location (0.51° ; two-tailed t -test: $t(16) = 2.09$; $p = 0.05$). There was no significant difference between the conditions for the long SOA (0.36° ; two-tailed t -test: $t(16) = 1.62$; $p = 0.13$).

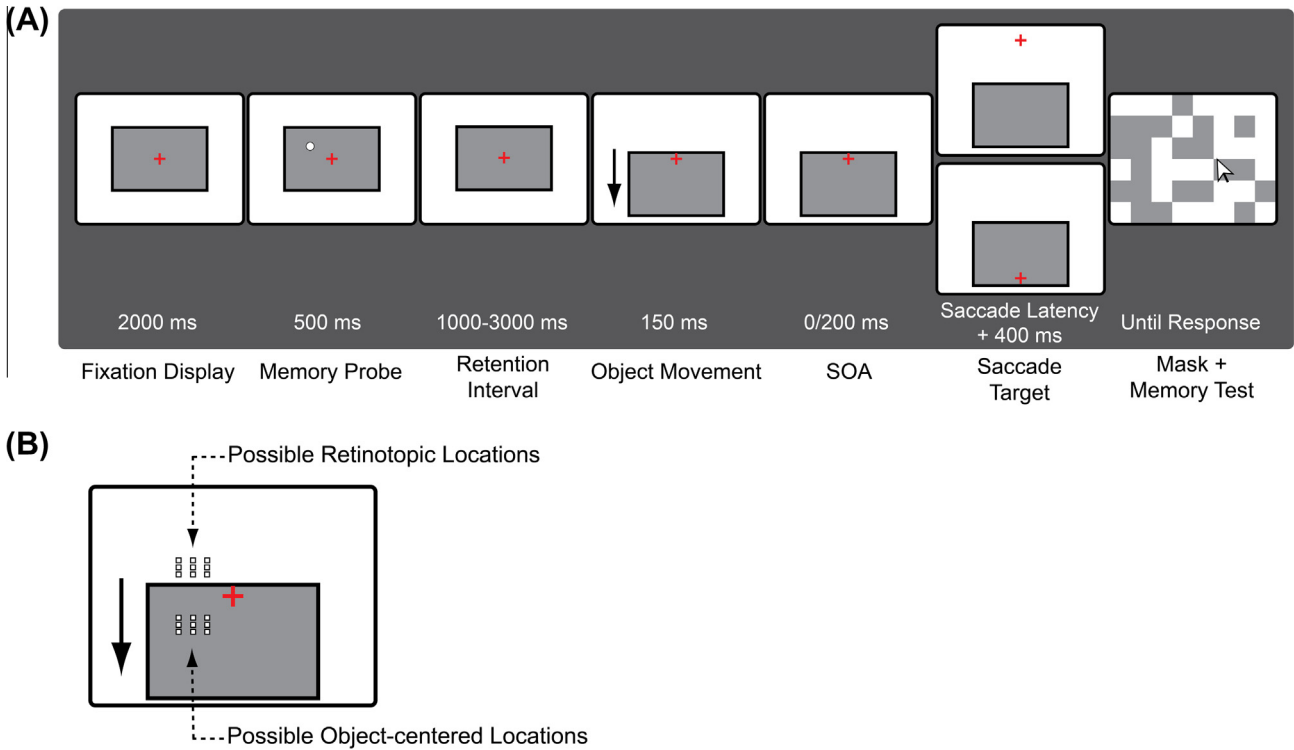


Fig. 1. (A) An example of a trial. Participants had to remember the exact location of the white dot relative to the object. After a retention interval the object moved either up or down (only down direction is shown). 0 or 200 ms after the movement of the object ended, an eye movement had to be made straight up or down. Saccades were made either into the same hemifield as the original, retinotopic location, or into the same hemifield as the updated, object-centered location. After a saccade was detected all stimuli remained on the screen for another 400 ms after which they were replaced by a mask. Participants had to indicate the updated memorized location with a mouse click. (B) Schematic illustration of all possible retinotopic locations of the memory cue in the top left quadrant and the corresponding updated, object-centered locations in the bottom left quadrant after the object moved downwards.

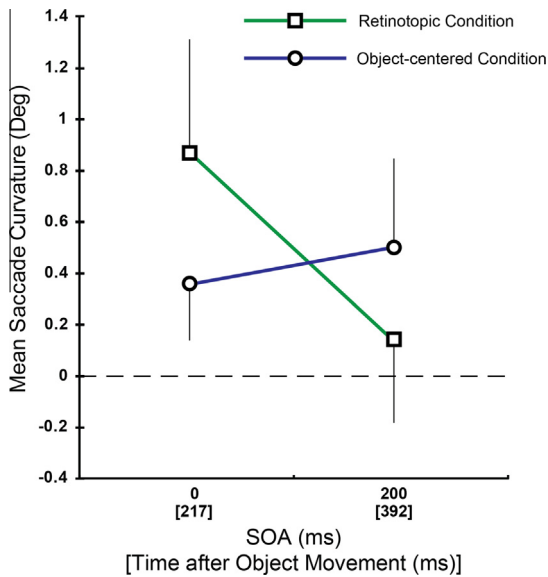


Fig. 2. Mean saccade curvature away from retinotopic (depicted in green) and object-centered (depicted in blue) locations for the short (0 ms) and long (200 ms) SOA. The average time after the end of object movement (SOA + saccade latency) is shown in square brackets. Error bars denote the 95% within-subject confidence interval (Loftus & Masson, 1994). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Participants' localization responses fell within 2.5° from the correct (object-centered) location on 78% of the trials. Responses in the localization task relative to the correct (object-centered) location are plotted in Fig. 4. As is clear from this figure, all

localization responses tended to cluster around the correct location. Only on a very few trials some participants clicked on the retinotopic locations or on a location in between the retinotopic and object-centered locations. Overall, there was an overshoot in participants' judgment of the correct location (1.78°). A repeated measures ANOVA on the localization responses revealed that localization error was higher in the object-centered condition ($F(1,16) = 15.35; p = 0.001$), probably because the object movement and eye movement were made in the same direction. There was no main effect of SOA ($F(1,16) = 2.93; p = 0.11$), nor a significant interaction between SOA and condition ($F(1,16) = 2.34; p = 0.15$).

In order to examine the precision of updating of the memorized location, the localization performance was analyzed as a function of the object-centered location. Since the amplitude of the object movement was variable it resulted in many possible object-centered locations. For this reason these locations were divided into six separate bins. Each bin contained on average 35 trials per participant. Fig. 5 shows these six bins, normalized to top right quadrant (colored squares). For each region the corresponding average localization performance is plotted (colored dots). Clearly, the localization performance follows the object-centered location, which indicates precise coding of the updated memorized location.

One could expect a relationship between successful updating of the memory representation during object movement and the accuracy of the subsequent localization response. To examine this hypothesis the distance between the indicated location and the correct location was determined for each trial. Subsequently a median split was performed on these localization errors, separately for each SOA, participant and condition. This resulted in two bins; one containing trials with a lower localization error and the other

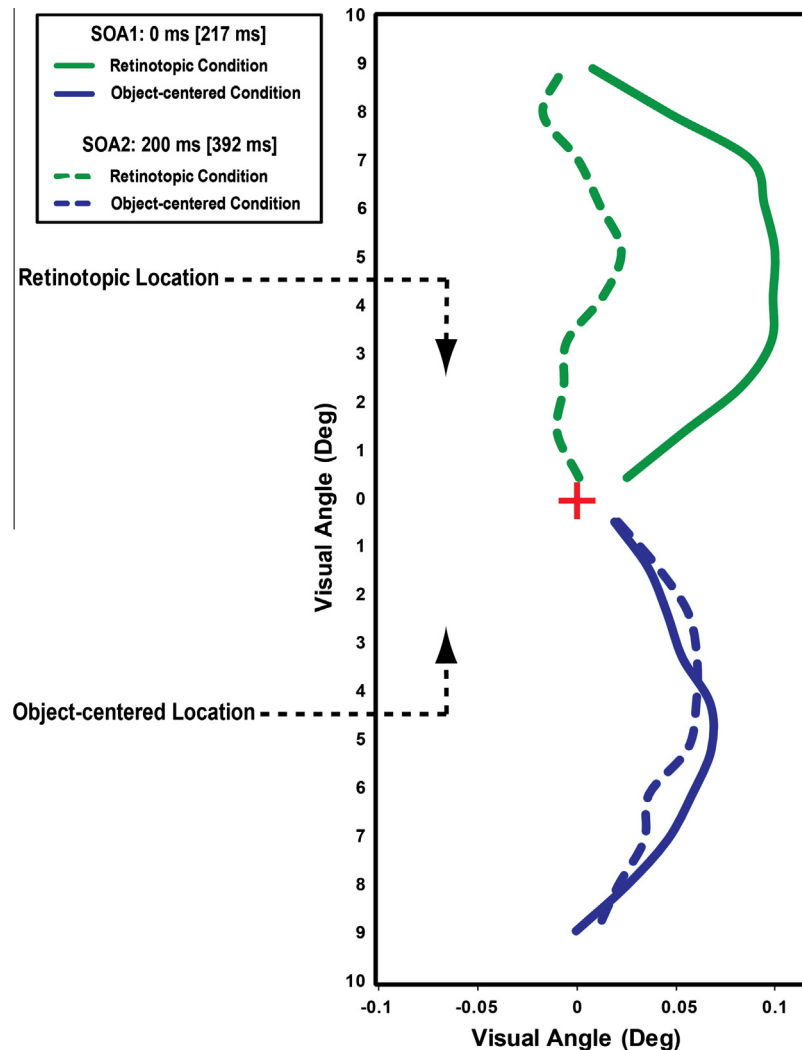


Fig. 3. Plot of average saccade trajectories along the retinotopic (depicted in green) and object-centered (depicted in blue) locations for the short SOA (0 ms, average saccade latency 217 ms) and long SOA (200 ms, average saccade latency 192 ms). Trajectories were normalized to the memory cue occurring on the left side and averaged across saccade directions and participants. Arrows indicate the average retinotopic and object-centered cue locations. Note that in order to illustrate saccade trajectories the X-axis has a larger scale than the Y-axis. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

containing trials with a higher localization error (Fig. 6). There was no three-way interaction between the accuracy, SOA and condition ($F(1, 16) = 1.05$; $p = 0.32$). Planned comparison for the more accurate trials showed no main effect of either condition or SOA ($F < 1$), but a marginally significant interaction between SOA and condition ($F(1, 16) = 3.48$; $p = 0.08$). For these trials post hoc analysis showed significant curvature away from both retinotopic (0.85° ; one-tailed t -test: $t(16) = 2.82$; $p < 0.01$) and object-centered locations (0.48° ; one-tailed t -test: $t(16) = 2.05$; $p = 0.03$) for the short SOA. For the long SOA, curvature away from the retinotopic location was no longer present (-0.06° ; one-tailed t -test: $t(16) = 0.20$; $p = 0.42$), while curvature away from the object-centered location remained present (0.86° ; one-tailed t -test: $t(16) = 2.29$; $p = 0.02$). Planned comparison for the inaccurate trials showed no significant interaction between SOA and condition ($F(1, 16) = 0.19$; $p = 0.67$), nor a main effect of SOA ($F(1, 16) = 0.06$; $p = 0.82$). The inability to accurately indicate the updated location corresponded with a retinotopic trace present at both SOAs (for the short SOA 0.74° ; one-tailed t -test: $t(16) = 2.01$; $p = 0.03$; for the long SOA 0.53° ; one-tailed t -test: $t(16) = 1.81$; $p = 0.04$), that did not subside over time (two-tailed t -test: $t(16) = 0.40$;

$p = 0.70$). This suggests that there might be a relationship between successful updating of a memorized location and the accuracy of the subsequent localization response.

4. Discussion

The current findings show that spatial memory representations are successfully updated during object movements. Immediately after the object stopped moving saccades curved away from both original retinotopic location of the memorized stimulus and updated object-centered location. Although early in time activity at the retinotopic location dominated, it diminished dramatically in the following 200 ms. In contrast, activity at the object-centered location stayed approximately the same or if anything slightly increased.

With every eye movement the objects around us fall onto a different part of the retina. According to the remapping hypothesis (Duhamel, Colby, & Goldberg, 1992), visual stability is preserved across these saccades by the transfer of activity between retinotopically organized neurons. Recently, similar remapping properties were found when updating spatial attention and working memory

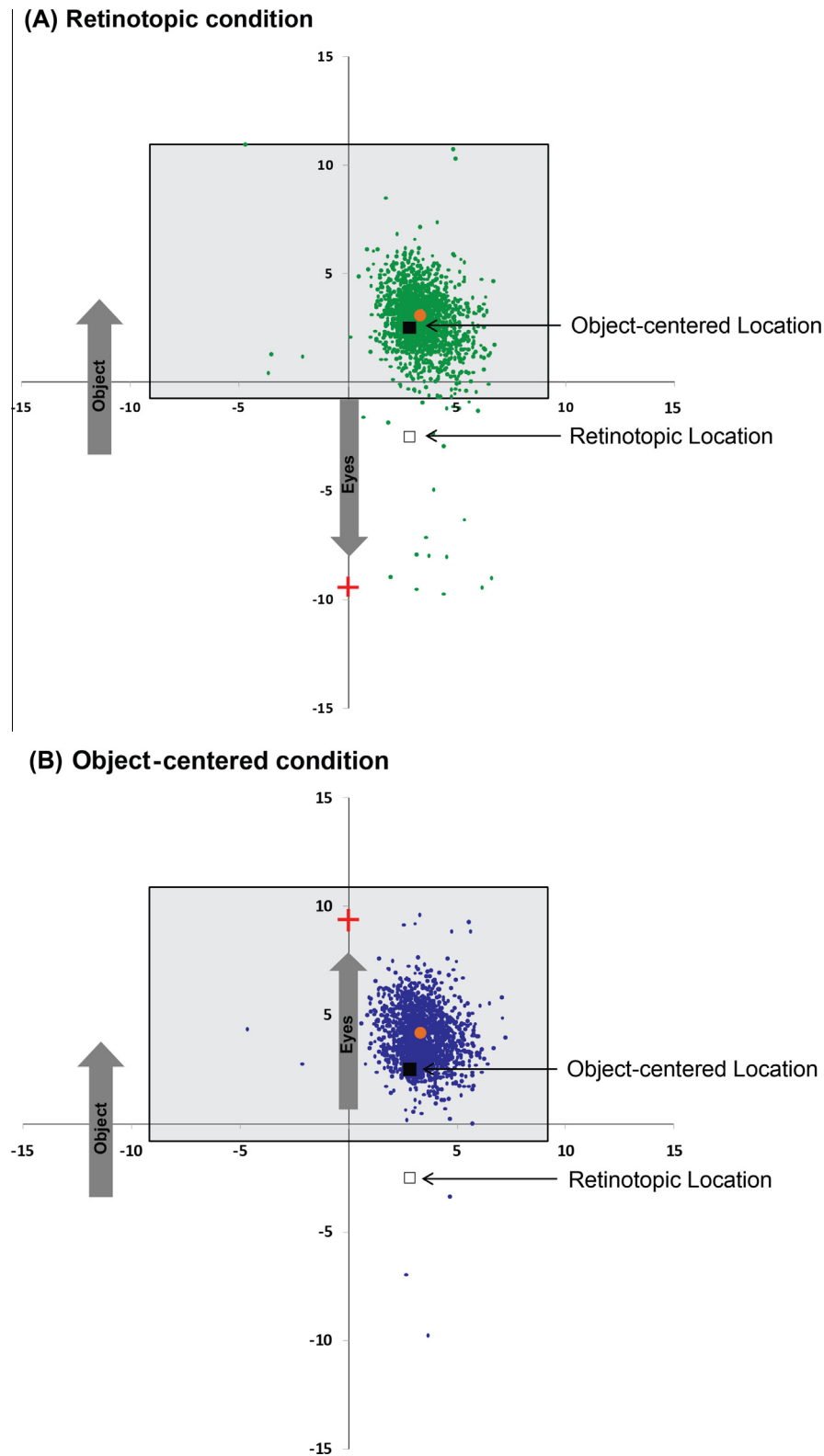


Fig. 4. The distribution of localization responses in the retinotopic (A) and object-centered (B) condition. For every trial the difference in X and Y position between the localization response and the correct (object-centered) location was calculated. These differences are plotted relative to the average object-centered location. The average retinotopic and object-centered locations are indicated by unfilled and filled squares, respectively. The average localization response in the two conditions is indicated by the orange dots. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

representations (Golomb, Chun, & Mazer, 2008; Mathot & Theeuwes, 2010; Rolfs et al., 2011). The efferent oculomotor signals, or the corollary discharge signals, are thought to be of crucial importance for this process (Sommer & Wurtz, 2008). However,

such signals are not available when updating a location on a moving object while the eyes remain stationary. Nevertheless, recent evidence shows that exogenous attention efficiently travels along with a moving object. Cueing a location on an object prior

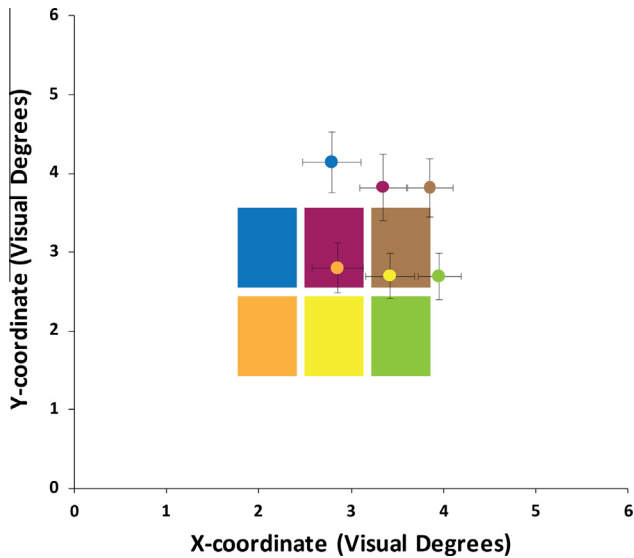


Fig. 5. The localization performance as a function of the object-centered location. All possible object-centered locations divided into six regions and normalized to top right quadrant (colored squares). For each region the corresponding average localization performance was plotted (colored dots). Error bars denote the 95% confidence interval. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

to its movement showed that attentional facilitation was present at the nonretinotopic, object-centered location directly after the movement (Boi et al., 2011). Interestingly, this facilitation was found to be larger at this object-centered location than at the retinotopic location. Similar effects were found for exogenously cuing a location on a rotating object (Theeuwes, Mathot, & Grainger, 2013). In line with these results we demonstrate that a location stored in working memory is also represented in the object-centered coordinates directly after the object movement. There seems to be efficient updating even when corollary discharge signals are not present.

Golomb and colleagues (Golomb, Chun, & Mazer, 2008; Golomb et al., 2010, 2011) used attentional facilitation to study updating of a memorized location during saccades. Retinotopic facilitation dominated spatiotopic facilitation directly following an eye move-

ment, but within 250 ms facilitation at the irrelevant retinotopic location decayed and facilitation at the spatiotopic coordinates became dominant. This pattern shows a striking resemblance with the way a memory representation was updated in our paradigm. Attention is known to play a role in both the coding and maintenance of information in spatial working memory (Awh, Vogel, & Oh, 2006; but see Belopolsky & Theeuwes, 2009), and given the tight relationship between these concepts both findings might be manifestations of the same mechanism of updating neural activity.

Even though it is not clear whether participants noticed it, the direction of object movement in our task was predictable. Therefore, it is possible that participants formed a prediction about where the updated location would be in advance of object movement. Since the amplitude of object movement varied unpredictably from trial to trial, this prediction had to be very crude. Even though possible, it is highly unlikely that participants used such a strategy. First, as can be seen in Fig. 5, localization responses systematically vary as a function of the object-centered location. This suggests that the representation of the updated location was rather precise. If the updated representation were coarse, then the localization responses should have been clustered around the center of gravity of all possible object-centered locations. Second, we found a relationship between the precision in the localization task and the updating of the memorized location as measured by saccade curvature (Fig. 6). On trials, where the localization was not precise we did not find curvature away from the object-centered location, indicating that on those trials updating was not successful.

Saccade curvature has been explained as a consequence of competition between potential saccade targets. Both attending to a location and the maintenance of a location in working memory seem to result in preparation of a saccade and the corresponding neural activity within oculomotor maps (Sheliga, Riggio, & Rizzolatti, 1994; Theeuwes, Olivers, & Chizk, 2005). If one needs to make a saccade to another location than the one kept in working memory, it is assumed that this oculomotor activity at the memorized location is inhibited. Subsequently, the inhibitory field in the saccade map causes the overall vector of the prepared saccade to shift in the opposite direction (Doyle & Walker, 2001; Sheliga, Riggio, & Rizzolatti, 1995). Our findings show that activity in the oculomotor map is also updated during object movement. This might be a consequence of updating taking place in higher areas, or possibly by remapping of neural activity within oculomotor structures, such

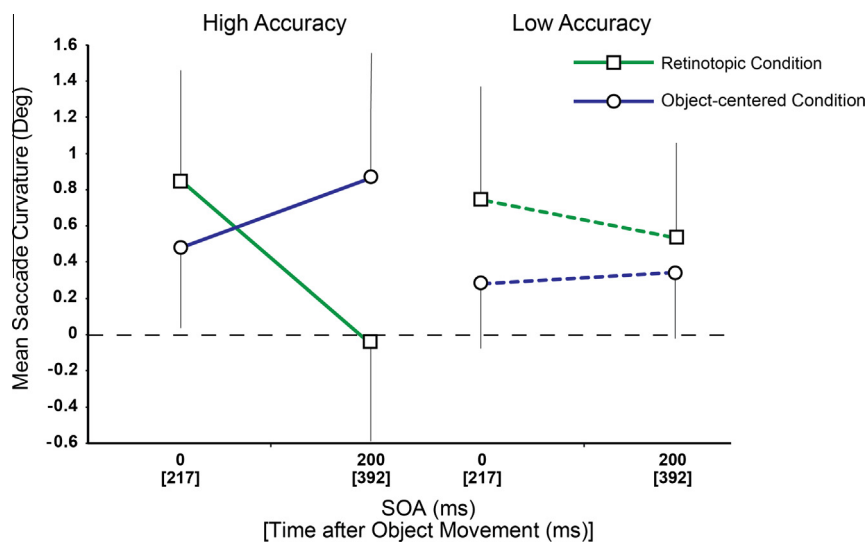


Fig. 6. Mean saccade curvature away in the retinotopic and object-centered conditions as a function of accuracy in the localization task. Left panel: High accuracy refers to the more accurate half of the trials, obtained after performing a median split on the localization errors. Right panel: Low accuracy refers to the more inaccurate half of the trials, obtained after performing a median split on the localization errors. Error bars denote the 95% within-subject confidence interval (Loftus & Masson, 1994).

as frontal eye fields (FEF) or superior colliculus (SC). Previous studies have shown such remapping properties in both FEF and SC neurons during saccades (Umeno & Goldberg, 1997; Walker, Fitzgibbon, & Goldberg, 1995), and a similar mechanism might underlie updating in the absence of eye movements. The temporary coexistence of both representations that was found might be a consequence of gradual remapping of activity from one location to the other.

Previous neurophysiological studies have convincingly shown that corollary discharge signals accompanying execution of eye movements were necessary to trigger remapping of receptive fields (Duhamel, Colby, & Goldberg, 1992; Umeno & Goldberg, 1997; Walker, Fitzgibbon, & Goldberg, 1995). In those studies, remapping was not observed when attention was shifted to saccade target without actually making an eye movement. However, there was also no need for remapping, since there was no change in retinal location of the attended input (visual or memorized). Despite the absence of a corollary signal in the current experiment, participants had to constantly update the memorized location during rapidly changing visual input. The results suggest that attention was crucial in the gradual transformation from retinotopic to object-centered representation, resembling the process of updating of receptive fields during saccades. In future studies it would be interesting to examine the evolution of reference frame transformations during object movement on a finer time scale. Specifically, it is important to understand whether updating to object-centered coordinates occurs already during object movement or starts shortly after the movement.

In summary, we have shown that working memory representations are successfully updated during object movement. Despite the absence of efferent signals about upcoming eye movements this updating occurs either during or very shortly after the movement was completed.

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