Updating visual–spatial working memory during object movement

Paul J. Boon *, Jan Theeuwes, Artem V. Belopolsky

Department of Cognitive Psychology, Vrije Universiteit, Amsterdam, The Netherlands

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 temporary 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.

* Corresponding author. Address: Department of Cognitive Psychology, Vrije Universiteit, Van der Boechorststraat 1, 1081 BT Amsterdam, The Netherlands. Fax: +31 20 598 8971.

E-mail address: p.j.boon@vu.nl (P.J. Boon).

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 chin-rest. A grey rectangular object with a width of 18.75 degrees of visual angle (°) 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 made 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: $t(16) = 1.62$; $p = 0.13$).