

The time course of spatial memory processing in the two hemispheres

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Received 8 April 2005; received in revised form 1 February 2006; accepted 3 February 2006

Available online 13 March 2006

Abstract

Previous studies have shown that memories for positions are often distorted in systematic ways, indicating the influence of categorical positions codes which can bias responses in object-relocation tasks towards stored spatial prototypes. In the present study, we examined the time course of these categorical influences. Subjects had to relocate the position of a tachistoscopically presented dot within a circle, which could appear in either the left visual field (i.e. initially to the right hemisphere) or the right visual field (i.e. initially to the left hemisphere). Three retention intervals between presentation and relocation were used: 500, 2000 and 5000 ms. Performance was most accurate with left visual field/ right hemisphere presentation. Systematic distortions were found for angular errors (dot relocations regressed towards the 45° with a quadrant) as well as for radial errors (dots were replaced in the direction of the circle's circumference, and this more so when the dot was further away from the circumference). Importantly, these categorical biases became stronger with retention interval and initial left hemispheric processing. These results suggest that categorical spatial coding might be the default manner in which spatial information is remembered over time. Finally, the left hemisphere may play an important role for such a categorical spatial coding.

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Keywords: Spatial memory; Hemispheric differences; Retention intervals

1. Introduction

Remembering the locations of objects in space has been claimed to encompass at least two distinct spatial codes (Huttenlocher, Hedges, Corrigan, & Crawford, 2004; Huttenlocher, Hedges, & Duncan, 1991; Laeng, Peters, & McCabe, 1998; Lansdale, 1998). First, there is a fine-grained code providing exact knowledge about the objects' positions. Second, a categorical spatial code represents the general spatial category in which an object falls. Spatial memory performance typically reflects the combined influences of the two codes. Evidence for the categorical codes follows from the fact that distortions in spatial memory are not simply random (which would indicate a unitary, but imperfect fine-grained coding mechanism) but show systematic distortions in the direction of what can be

argued to be categorical prototypes. In a "classic" task that has been used in many studies thus far, and it was also employed in the present study, subjects have to reconstruct the location of a single dot in a circle. The relevant spatial categories are formed by the circle's (invisible) quadrants. Prototypical category values attract the reconstructed location towards the centre of the quadrant (angular bias) in which it was originally presented and towards the circle's perimeter (radial bias).

Interestingly, the foregoing dual code distinction can easily be linked to the distinction between coordinate and categorical coding of spatial relations in perception made by Kosslyn and others (Jager & Postma, 2003; Kosslyn, 1987; Kosslyn, Chabris, Marsolek, & Koenig, 1992; Laeng & Peters, 1995). Coordinate spatial relations capture precise, metric information needed amongst others to guide spatiomotor actions. In turn, categorical spatial relations provide abstract, invariant information about visual constellations, allowing a degree of constancy to perspective changes. One important further implication of Kosslyn's idea was that coordinate spatial processing would engage more right hemisphere processing, whereas categorical processing would depend more on left hemispheric resources. Laeng

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et al. (1998) applied this lateralization hypothesis successfully to the domain of spatial memory. In a visual half field study, they showed that systematic biases in positional reconstruction from memory – supposedly reflecting categorical coding – were stronger with lateralized stimuli presentations to the left hemisphere.

Assuming that indeed two spatial memory codes in combination determine how well we are able to reconstruct the locations of previous events, an important question concerns the time course of these coding mechanisms. Moreover, if we further assume that different neural circuitries are involved as well, it clearly would be of interest to explore the temporal characteristics of spatial processing within each hemisphere. Werner and Diedrichsen (2002) recently looked at the presence of categorical distortions in spatial memory on the very short time scale, i.e. within a few 100 ms after presentation. They observed that categorical distortions already occurred with retention intervals as brief as 50 ms. One possible interpretation of these findings is that, already during the perceptual phase, categorical and coordinate spatial mechanisms run in parallel and they automatically influence spatial memory.

The goal of the present study was to examine the time spectrum of these effects in more detail. In other words: what happens to categorical spatial memory codes as time passes? To answer this question, we compared performance on the dot in circle memory task for short intervals (500 ms) to intermediate duration intervals (2 s) to relatively ‘long’ periods (5 s). We may speculate here about three possible outcomes. One could be that categorical biases not only emerge very rapidly (see Werner & Diedrichsen, 2002) but also persist in time. For instance, categorical coding would be useful because it provides a way to infer and maintain the invariants from a continuously changing environment. A second possibility could be that categorical codes decline after some time. One likely pattern could be that systematic errors are replaced by (larger) random errors over time. Finally, the influence of categorical biases could actually become larger over time, because this memory is more resistant to decay than the spatial memory of the actual coordinates. In other words, eventually people may just remember the prototypes and not the specific instances any longer.

2. Methods

2.1. Research participants

Twenty-four students of the Utrecht University participated, 12 males and 12 females. They varied in age from 20 to 26 years, and were all right-handed. All participants had normal or corrected to normal vision, and none suffered any subjective memory or attention complaints.

2.2. Materials and procedure

Subjects were seated 39 cm from a 17 in. computer monitor. Their head was fixed in a chin rest and head clamp. They fixated on a fixation cross in the middle of the screen at eye level. Their task was to click with the computer mouse on the middle of the fixation cross to start an experimental trial. Next, a grey circle with a black circumference of 9 cm diameter appeared against a grey background, with the centre of the circle either 15° to the left or to the

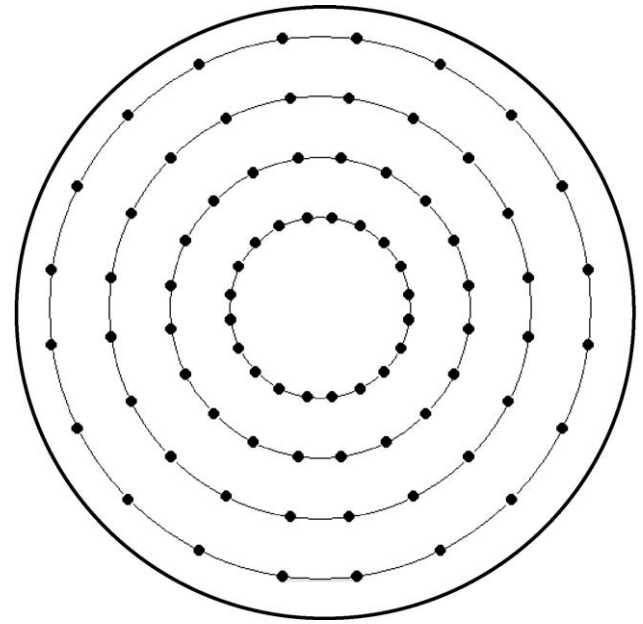


Fig. 1. The 80 possible dot locations within the circle. Notice that circles within the bold perimeter were never really shown.

right of fixation. The circle contained a black dot of 0.1 cm diameter which was located in one out of 80 possible positions (see Fig. 1). The dot's position varied according to a 4 (quadrant) $\times$ 5 (angle within quadrant, 8°, 26.5°, 45°, 63.5° or 82°, respectively) $\times$ 4 (radial location within angle, being 0.3, 0.5, 0.7 or 0.9 of the radius from the centre of the circle, respectively) design. The 8° was close to the vertical axis in all quadrants, whereas the 82° was close to the horizontal axis in all quadrants. Notice that the centre of the circle was never marked.

Dot and circle were presented for 85 ms. After a delay of 500, 2000 or 5000 ms the circle reappeared (always in the same horizontal position as originally presented). Subjects were instructed to relocate the position of the dot as well as they could using the mouse cursor. Subsequently, the next trial started.

A dot appeared only once in one of the 80 possible locations within the circle. Accordingly, there were 80 trials in each visual for each retention interval, making a total number of 480 trials. Order of locations within the circle and of the circle within the left and right visual field was randomised. Subjects performed three blocks, each block corresponding to one of the retention intervals. Order of retention intervals was counterbalanced over subjects.

3. Results

3.1. Angular differences

An analysis of variance was conducted with hemisphere (left, right), retention interval (500, 2000 and 5000 ms) and quadrant angle (8°, 26.5°, 45°, 63.5° or 82°) as independent variables, and angular deviation (i.e. difference between presented angle and relocated angle) as the dependent measure. Notice that with regards to biases towards spatial prototypes, a negative angular deviation would mean an error towards the 45° for angles smaller than 45°, whereas such a bias would be expressed as a positive angular deviation accuracy deviation for angles larger than 45°. Importantly, there was a significant hemisphere main effect ($F[1,23] = 5.80$, $p = .02$). Errors were larger when the dot presentation and relocation took place under initial left

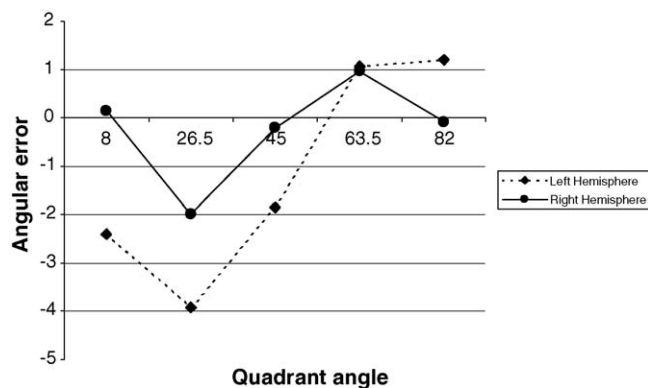


Fig. 2. Average angular errors across the five presented angles within a quadrant within the two hemispheres.

hemisphere control (i.e. in the right visual field): -1.18 for the left hemisphere versus -0.24 for the right hemisphere.¹

Interestingly, quadrant angle also yielded a significant main effect ($F[4,92] = 7.9, p < .001$). As clearly can be seen in Fig. 2, errors were minimal for dots presented with a 45° angle. Deviations in positive direction for presented angles larger than 45° , and in negative directions for presented angles smaller than 45° mean that angles are being remembered closer to 45° than they actually were. This confirms the systematic bias tendency in spatial memory. Moreover, there was an interaction of hemisphere by angle ($F[4,92] = 4.34, p < .01$). While this interaction is rather complex, Fig. 2 appears to suggest that the angle differences are slightly stronger in the left hemisphere.

Retention interval did not yield a significant main effect ($F[2,46] = .33, p = .72$). The interaction between retention interval and angle was not significant either ($F[8,184] = 1.8, p = .08$). Most importantly, the interaction hemisphere by retention interval was highly significant ($F[2,46] = 7.33, p < .01$). Fig. 3 shows that the hemispheric differences favoring the right hemisphere over the left hemisphere increased with delay. Within-subject's contrasts showed a linear significant trend over retention interval for the right hemisphere ($p = .024$; polynomial contrasts), indicating an improvement with time. There was also a significant linear trend over retention interval for the left hemisphere ($p = .001$; polynomial contrasts), only this time in the reversed direction. Angular errors increased with delay for the left hemisphere.

Finally, the interaction hemisphere by quadrant angle by retention interval was not significant.

3.2. Radial differences

A second analysis of variance was conducted with hemisphere (left, right), retention interval (500, 2000 and 5000 ms)

¹ As pointed out by an anonymous referee, the most rightwards dot locations in the right visual field (i.e. left hemisphere) and the most leftwards dot location in the left visual field (i.e. right hemisphere) are rather eccentric. Comparison of average distance errors for the dot locations from the most eccentric circle half to those residing in the less eccentric half did not yield significant effects. So circle half eccentricity was not included in the subsequent analyses.

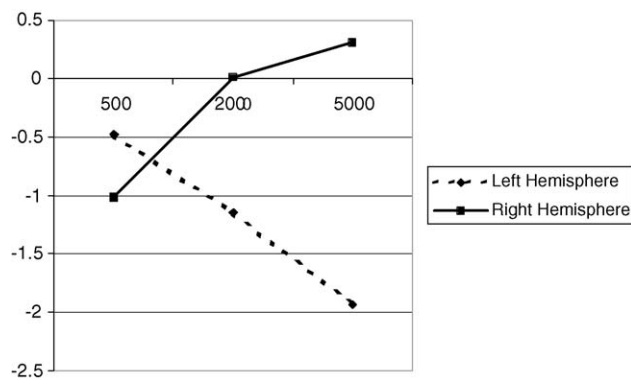


Fig. 3. Average angular errors in the two hemispheres over the three retention intervals.

and radial location (.3, .5, .7 and .9 radius) as independent variables, and radial deviation (i.e. difference between presented radial location and relocated radial location) as the dependent measure. Again, there was a significant hemisphere main effect, $F[1,23] = 9.37, p < .01$. Radial errors were largest when stimuli were initially under left hemisphere control (i.e. $-.12$ versus $-.11$, for the left and right hemisphere, respectively).

Interestingly, radial location also yielded a significant main effect, $F[3,69] = 115.3, p < .001$. As shown in Fig. 3, errors were smallest for dots presented with a .9 radial location. Deviations increased in negative direction with smaller presented radial location. In other words, there was a tendency to place the dots closer to the perimeter of the circle and this tendency became larger the further away the dot's original distance from the perimeter. The interaction of hemisphere by radius was not significant, $F[3,69] = 1.99, p = .12$.

Retention interval yielded a significant main effect on the radial errors, $F[2,46] = 6.3, p < .01$. Performance decreased from 500 to 2000 ms retention interval (within-subject's contrast: $p = .002$). It remained stable between 2000 and 5000 ms ($p = .80$). There was also a highly significant retention interval by radius interaction, $F[6,138] = 13.75, p < .001$. Fig. 4 indicates that the radial bias effect – i.e. the tendency to misplace the dots more in the direction of the perimeter the further away

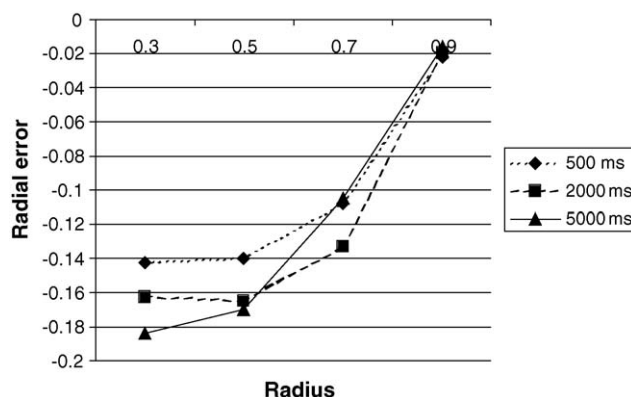


Fig. 4. Average radial errors across the four radial positions for the three retention intervals.

they are from the boundaries of the circle – was more pronounced with longer delays (i.e. 2000 and 5000 ms). Neither the interaction hemisphere by retention interval was significant, nor the interaction hemisphere by retention interval by radius.

4. Discussion

What happens to our memory of position when time passes? The present study specifically examined the nature of the spatial codes used to relocate items in space. In particular, we focused on the development of these codes over time. Subjects were briefly shown a circle containing a dot in either the left or the right visual field, and subsequently had to relocate the dot in the empty circle, which was placed in the same visual field. A main finding was that spatial memory performance is biased in a systematic manner. Angular errors typically were in the direction of 45° angle within a quadrant of the circle. Radial deviations were always towards the circle's perimeter. This tendency was stronger when the dot's location originally was further away from the perimeter. These results collaborate those obtained by Huttenlocher et al. (1991, 2004), Laeng et al. (1998) and Nelson and Chaiklin (1980). Apparently, the representations we make of space tend to be organized around both imagined (i.e. 45° centre of mass within the quadrants) and physical (i.e. the perimeter) prototypes.

Importantly, these systematic distortions were affected by time. A significant retention interval main effect was observed for the radial bias (tendency to misplace dots towards the perimeter and more strongly so when the original position is further from the perimeter). Radial bias increased with delay. Werner and Diedrichsen (2002) showed that categorical distortions in spatial memory already emerge after as soon as 50 ms. The present results indicate that categorical influences may increase with time. In line with these results, Hubbard and Ruppel (2000) also reported stronger landmark attraction effects of memory for the locations of stationary targets when the landmark was no longer visible.

Previously it has been suggested that biases in spatial memory might largely depend upon categorical coding mechanisms in the left hemisphere (Laeng et al., 1998). The marked hemisphere effects in the present study corroborate this suggestion. Both angular and radial errors were strongest in the left hemisphere. Of particular importance, there was a highly significant hemisphere by retention interval interaction for the angular errors. The performance difference between the two hemispheres grew larger with the passing of time. Angular errors became particularly large for the longest delays in the left hemisphere. We may interpret this as evidence that the role of categorical position encoding within the left hemisphere accumulates with time.

The idea that the left hemisphere plays a special role in maintaining spatial codes would be further confirmed by observing a hemisphere by angle interaction or a hemisphere by radius interaction. The former interaction indeed was significant. Larger angular differences were found in the left hemisphere, indicating a greater tendency to code information into prototypical values.

The interaction hemisphere by radius failed to reach significance, though.

In conclusion, the current results show that systematic biases can play a substantial role when remembering locations in space. These biases may not only emerge rather early in processing, but they may also continue to grow over time. Speculatively, it might be that eventually only the memory of the prototypical spatial values remains. The persistence of spatial category information over time is illustrated by real life situations where landmark information becomes readily available when reproducing a particular route. Especially, the left hemisphere could be important in implementing the categorical spatial codes. In contrast, the exact metrics of positions may be more dependent on right hemisphere's functioning. This perspective is consistent with the "classic" view that the right hemisphere is more specialized in processing of metric information (Jager & Postma, 2003; Kessels, Kappelle, de Haan, & Postma, 2002; Kosslyn, 1987; Kosslyn et al., 1992; Laeng et al., 1998). Interestingly, certain differences existed between the radial bias patterns and the angular bias patterns. In the present dot-in-the-circle task the former depended on real, physical elements of the figure (i.e. the circle's circumference), which acted as prototype locations, the second involved imaginary prototypes (i.e. the central oblique line within a circle's quadrant). Thus, one may surmise that the way categorical spatial biases develop and are deployed might be determined by whether they have a physically real origin or merely exist in one's mind.

Acknowledgement

This study was supported by a PIONIER research grant to A.P. (NWO #440-20-000) from the Netherlands Organization for Scientific Research (NWO).

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