Lateralization of Route Continuation and Route Order

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Abstract. Navigation is a complex cognitive ability and its structure is still poorly understood. Memory for route continuation and route order are hypothesized to be at least partially separate components of navigation ability. In the current experiment, participants studied a route in virtual reality. The dissociation between route continuation ("what turn did you make here?") and route order ("which object did you see first?") was tested in a visual half field paradigm, to assess lateralization patterns. Route continuation showed a left visual field advantage and route order a trend for a right visual field bias. This outcome further substantiates a dissociation between spatial and spatiotemporal aspects of navigation in humans.

Keywords: Lateralization, navigation, continuation, order memory.

1 Introduction

Finding our way around is a complex ability, consisting of a range of cognitive activities. When we interact with our environment, we store various types of information about the landmarks we encounter, for example (see e.g. [1,2]). When we receive descriptions on how to find a particular location in a new city, these will commonly entail sentences like 'when you reach the train station turn left, and when you have passed the supermarket, walk straight ahead until you reach the museum'.

Landmarks are therefore linked to different types of information, not only do we process their identity, but also properties like route continuation, which turn to take at a specific location, and route order, the order of items along a route, are dealt with during navigation. Analogous to general studies on memory (e.g. [3,4,5,6]), a clear dissociation between recognition and order memory has been reported during navigation as well (e.g. [7]). Moreover, this dissociation has been extended to route continuation and route order [8]. Given the complexity of navigation ability, the attempt to identify separate elements of this ability is clearly useful. Theoretically, an overview of the separable elements is vital to better understand navigation, which in turn can explain for individual differences in navigation ability (e.g. [1,9]). Clinically, such dissociations can help in the diagnosis and even treatment of specific impairments within the navigation domain [10]. In particular, memory for order has received little attention as a potentially separate element of navigation, although several studies highlight the functional isolation from spatial forms of memory. Memory for route continuation is an explicitly spatial process, whereas route order memory comprises

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both temporal and spatial information. The amount of studies focusing on the dissociation between these spatial and spatiotemporal aspects of route memory is limited [7,8]. With the current study we therefore aim to shed more light on the nature and extent of this dissociation with regard to its underlying processing mechanisms.

The hippocampus is the key brain structure when creating mental representations of an environment (e.g. [11,12,13]). This mental representation appears essential for answering questions concerning routes taken through an environment. Moreover, within the hippocampus a division has been made between the left and right side of the hippocampus. Igloi and colleagues [14] have studied lateralization patterns within the hippocampus and suggest that memory for places is lateralized to the right, and memory for temporal sequences to the left, which is closely related to our current research question. They interpret place memory and sequence memory as reflecting allocentric, or environment-based, processing and egocentric, or observer-based processing, respectively.

Comparing lateralization patterns is very useful for examining the distinction between route continuation and route order: if they differ in their lateralization pattern, this provides further support that there are at least partially separate underlying mechanisms to these types of memory. Therefore, in the current study we applied a visual half field design to examine potential lateralization patterns for both route continuation and route order. A visual half field design allows for a comparison of behavioral responses to stimuli presented briefly to the left visual field to responses to stimuli presented briefly in the right visual field. These responses are thought to reflect contralateral processing in the cerebral hemispheres; left visual field performance therefore reflects right hemisphere processing and vice versa (see e.g. [15]. The outcomes of the study by Igloi and colleagues provide a first suggestion that different lateralization patterns could exist. Yet, place memory as tested in [14] is explicitly allocentric. This means that for this type of memory, the external environment is consulted in order to identify locations in the environment. The spatial task of route continuation, deciding which turn to take at specific points along the route, is egocentric: the decision to go left or right is dependent on the observer's position. Moreover, there is a possibility, albeit unlikely, that the left lateralization of the sequences in their egocentric task is related to verbal coding of the turns to be taken to reach a destination, e.g. 'left, right, right, left'. Such verbalization might activate language related areas in the brain, which are typically left lateralized. In a typical route order task, participants are asked to compare specific elements of a route, based on the moment they encountered them along the route. Such comparisons are less likely to be linked to verbalization as a large number of possible combinations of elements can be presented, which cannot be labelled verbally in simple terms.

Therefore, two questions arise when translating the lateralization pattern found in [14] to route continuation and route order memory: 'Does the right hemisphere advantage for place memory generalize to the egocentric spatial task of route continuation?' and 'Does the left hemisphere advantage for sequences also emerge when verbal coding is an impossible strategy?' If memory for places is lateralized to the right, regardless of the perspective needed to perform the task, a right hemisphere bias for route continuation is expected. Alternatively, if the type of perspective used is crucial for the lateralization pattern, then route continuation should be left lateralized as it makes use of an egocentric perspective. If the left hemisphere advantage found for sequences is not based on the potential verbal nature of the task, but on the processing of order of items, then a left hemisphere advantage is expected for route order. If verbal processing is essential for the direction of lateralization, then route order memory should not show lateralization to the left. Moreover, if route continuation and route order differ in their lateralization pattern, this further supports a clear distinction between these two types of route memory.

2 Methods

2.1 Participants

In total, 35 participants (9 male) took part in the experiment, with a mean age of 22 (range 19-28). Right-handedness was ensured for all participants, as measured with a Dutch version of the Edinburgh Handedness Inventory [16], with a mean score of 77.6 (SD=34.6, range 47-100, on a scale of -100, extremely left-handed, to +100, extremely right-handed). All participants were students and participated in exchange for course credit. All participants had normal or corrected to normal vision and were unaware of the rationale of the experiment.

2.2 Task Design and Materials

The experiment consisted of a video of a virtual maze in which fifteen different objects were placed and three tasks that assessed memory of the route in different ways. First of all, participants were tested on recognition of these objects. Next, they were tested on their knowledge of route continuation, and their order memory.

A 3D virtual maze was created in Blender (Blender Foundation, the Netherlands). The objects in the maze were selected from the Bank of Standardized Stimuli (BOSS, [17]). Everyday objects were selected that were easy to identify. In the tasks, the dimensions of these objects were 300 * 450 pixels. In Figure 1A a screen shot from the video is shown, in which of one these objects is visible. A path was selected in the maze consisting of thirteen turns and fifteen objects. This path was shown in the video through the virtual environment. A map of the route through the virtual environment, along with dots depicting the object positions is shown in Figure 1B.

The tasks were programmed in OpenSesame [18]. After the first instructions, participants started with the recognition task. This task consisted of three practice trials and 30 experimental trials. The trial sequence was as follows: Fixation cross (2000 ms), stimulus (150 ms), response window (until response is given). All items were presented centrally. The practice trials were inserted to expose the participants to the speed of presentation of the stimulus. Therefore, during practice, the stimuli were black squares. In the experimental trials, all fifteen objects along the route were presented, as well as fifteen distractor objects.

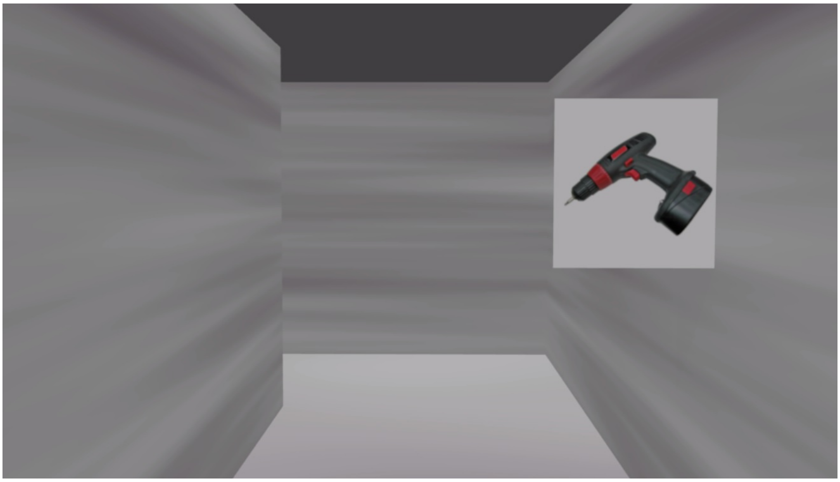


Fig. 1. A. Screenshot taken from the video, with a power drill as an object, after which a left turn was taken

The route continuation task also consisted of three practice trials and 30 experimental trials. The trial started with a central fixation cross (2000 ms), followed by an arrow pointing either to the left, to the right, or up (150 ms), next another fixation cross was presented (1000 ms), followed by a lateral presentation of the stimulus (150 ms), lastly the response window appeared for 3000 ms. The instruction was to indicate whether the direction of the arrow matched the direction of the route directly after the object shown. The objects were presented at a visual angle of 3 degrees, measured from the inner edge of the figure to the center of the screen. In this presentation, the objects were shown in isolation, without any informative background. Each of the fifteen objects on the route was presented twice. In the practice trials, the stimulus was a black square, instead of one of the objects.

For the order task also three practice trials and 30 experimental trials were created. The trial sequence was: central fixation cross (2000 ms), first stimulus presented centrally (150 ms), fixation cross (1000 ms), second stimulus presented laterally (150 ms), response window (3000 ms). The instruction was to decide whether the two serially presented objects were in the correct order, as encountered on the route. Again, the objects presented laterally were at a visual angle of 3 degrees, from the inner edge of the object to the center of the screen. Also, the objects were again shown in isolation, without any informative background. Each of the fifteen objects was used twice as a first object and twice as a second object. In the practice trials, the first object was a black square; the second object was a red square. The trialsequence of each of the three conditions is depicted in Figure 2.

For all three tasks, chance level was at 50% and participants responded with the arrow keys on a regular keyboard that were marked green ('correct') and red ('incorrect'). The video and tasks were presented on a 30-inch monitor, with a resolution of 1920 * 1200 pixels. Participants were seated 60 cm away from the screen and used a chin rest placed exactly in front of the center of the screen.

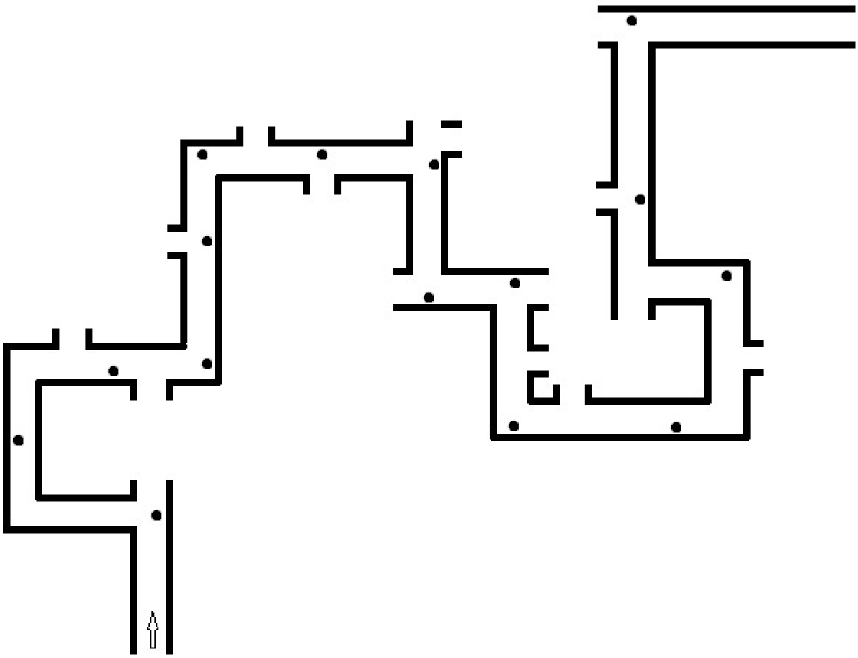


Fig. 2. B. A map of the route shown in the video. Dots represent object positions.

2.3 Procedure

Prior to participation, all participants signed an informed consent form. Next, they were orally instructed about the different parts of the experiment. The first part of the experiment was the viewing of the video. They were instructed to remember as much as they could from the video, without specific mention of the tasks that would follow. All participants viewed the same video three times.

After viewing the video, all participants were presented the recognition task. Next, either the route continuation or the route order task was presented first, followed by the other of the two tasks. The order of these two tasks was randomized across participants. Each task was preceded by an instruction on the screen, as well as an oral instruction to ensure correct understanding of the task for all participants.

2.4 Analyses

For all conditions, mean accuracy (Acc) and response time (RT) were calculated. Participants with an overall Acc at or below 50% were excluded from that particular task. At an individual trial level RT below 200 ms and above 3000 ms were excluded. The performance on the recognition task was used as an indication of how well participants had memorized the objects on the route. Sufficient recognition (at least 80% correct) was considered a prerequisite for informative performance on the route continuation and route order tasks.

Performance on the route continuation and route order tasks was analyzed by means of a repeated measures general linear model (GLM). Visual field (left, right) and task (route continuation, route order) were included as within subject factors in this GLM. This analysis was performed for both the Acc and the RT. Significant effects were followed up with Bonferroni corrected post hoc tests.

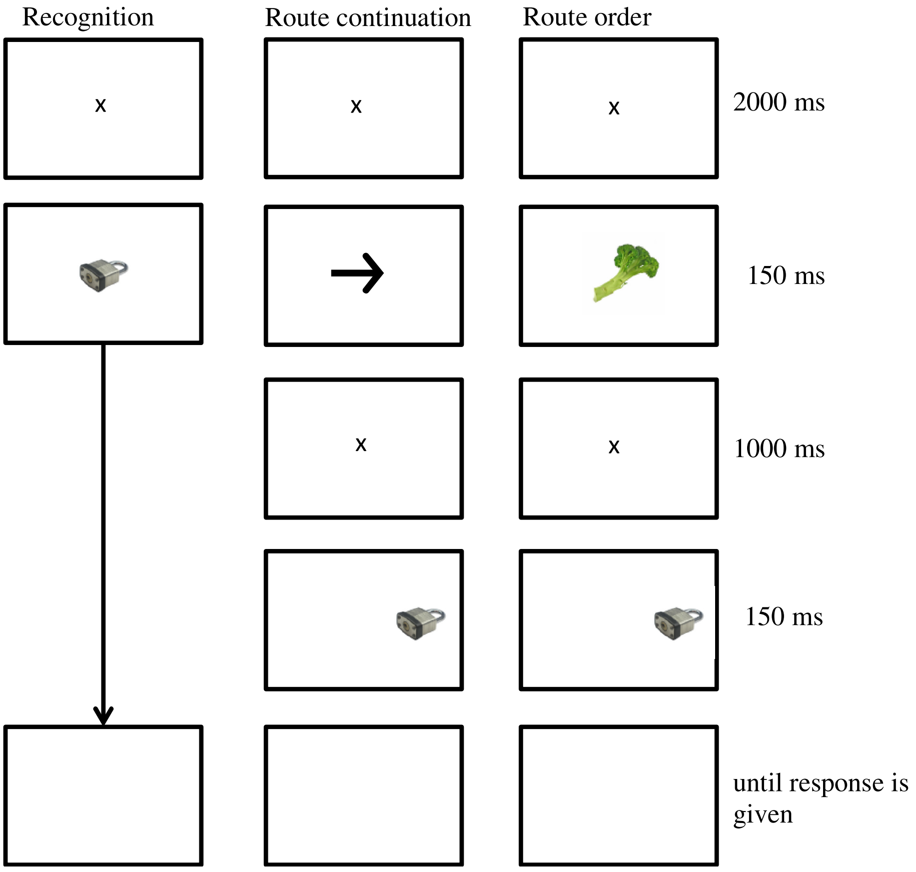
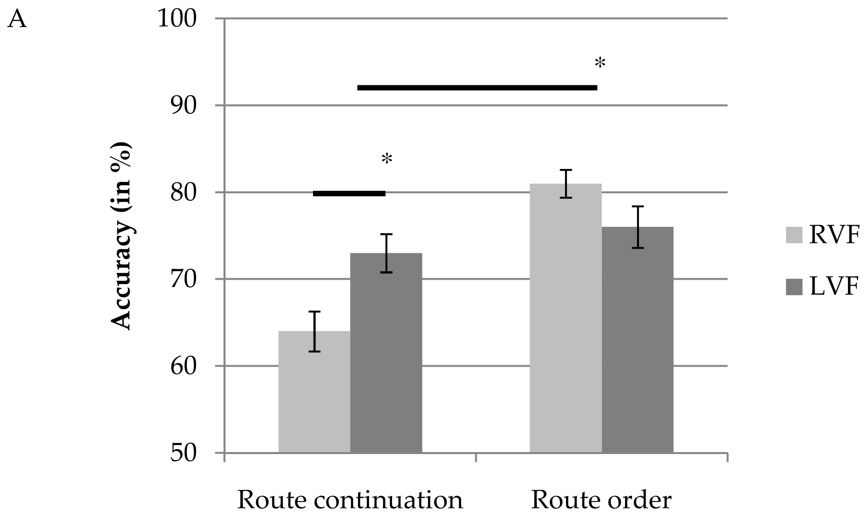


Fig. 3. Trial sequence for each of the three conditions

3 Results

First of all, the performance on the object recognition was assessed. The mean Acc of all participants was 93.3 % (SD=5.0, range 80-100%), with a mean RT of 681.3 (SD=138.8). For the route continuation task four participants had Acc values at or below chance level and were therefore excluded, for the route order task, one participant was excluded because of chance level Acc. The mean Acc and RT for both the route continuation and route order tasks are depicted in Figures 3A and B.



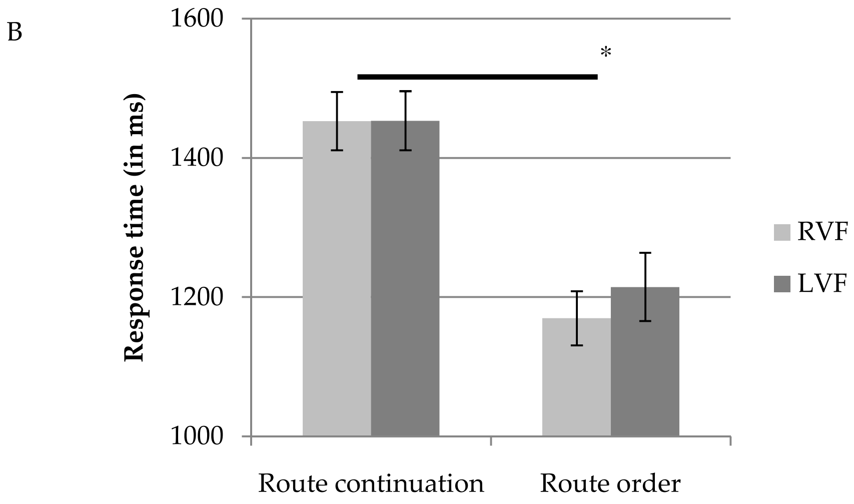


Fig. 4. Mean A) accuracy in percentage and B) response times in milliseconds for both the route continuation task and the route order tasks. Performance is split up by visual field. RVF=right visual field, LVF=left visual field. Error bars represent standard error of the mean (SEM). $*p<.001$

A repeated measures GLM including visual field and task was performed on Acc and showed a significant main effect of task, $F(1,29)=13.55$, $p=.001$, partial $\eta 2=0.318$. Performance was significantly better for the route order task, in comparison to the route continuation task. Additionally, a significant interaction of task and visual field was found, $F(1,29)=13.23$, $p = .001$, partial $\eta 2=0.313$. Follow up analyses showed that for route continuation, the difference between RVF and LVF was significant ($p=.001$). For route order this difference was at trend level ($p=.077$). For route continuation, performance reflected a right hemisphere advantage, whereas the trend for route order showed a left hemisphere advantage.

The repeated measures GLM for RT showed the same significant main effect for task, $F(1,29)=41.23$, $p < .001$, partial $\eta 2=0.587$. Responses were faster for the route order task. No other effects were significant.

4 Discussion

To further unravel the cognitive structure of navigation, we compared the lateralization patterns of both the spatial process of route continuation and the spatiotemporal process of route order. Although only few, previous studies have suggested that these processes are dissociated [7,8]. Furthermore, lateralization in hippocampal activation has been reported with a right hemispheric bias for place memory as well as a left hemispheric bias for sequence memory [14]. Route continuation can be interpreted as making use of place memory, and order memory is very similar to sequence memory. Therefore, we expected memory for route continuation and route order to be dissociated, as expressed by differential hemispheric lateralization.

Participants memorized a route through a virtual maze with objects placed along the route. Sufficient object memory was ensured for all participants with an object recognition task. The results of the subsequent route continuation and route order tasks showed that these two tasks were related to divergent patterns of lateralization, as there was a strong interaction of task and visual field. A significant left visual field, or right hemisphere, advantage was found for the route continuation task, whereas a trend for a right visual field, or left hemisphere, advantage was present for the route order task. These lateralization effects further confirm a dissociation between these two types of route knowledge.

Importantly, the tasks used here differ from those used in [14], in which case an allocentric place memory task was contrasted with an egocentric sequence task. In the current task design, both tasks were egocentric and concerned route knowledge, disregarding allocentric processing. Therefore, the current results allow for further speculation; the right hippocampus might be responsible for egocentric processing as well, depending on the precise task requirements. Furthermore, the possible criticism of a verbal strategy being present in the egocentric sequence task in [14] is not applicable for the current task, as participants directly compared two objects from the route and indicated whether their order was correct. This process most likely does not rely on verbalization of the spatiotemporal information from the route, as the task design allows for many possible combinations of stimuli, for which some form of verbal coding of order would be very inefficient.

It should be noted that this type of distinction is likely not restricted to the hippocampus and that lateralization as tested with a visual half field paradigm reflects lateralization patterns of the brain as a whole. Our results indicate that there is a dissociation in terms of lateralization, at a cerebral hemisphere level.

The current outcomes further substantiate previous findings of a dissociation between the spatial and spatiotemporal aspects of route memory. Not only are they functionally dissociated as previous studies showed, but the current results reveal a clear hemispheric dissociation as well; spatial route memory is lateralized to the right, while there is a trend for a left hemispheric bias for spatiotemporal route memory. Future studies should be directed at identifying the precise areas of the brain involved in these tasks. As [14] indicates, the left and right hippocampi are primary candidates for the current lateralization pattern.

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