



# Spatial Survey Estimation Is Incremental and Relies on Directed Memory Structures

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**Abstract.** This study examined how navigators of large-scale environmental spaces come up with survey estimates of distant targets. Participants learned a route through a virtual city by walking it multiple times in one direction on an omnidirectional treadmill. After learning, they were teleported to intersections along the route and pointed to multiple other locations. Locations were always queried in chunks of related trials relative to a participant's current position, either to all locations route forwards or all locations route backwards. For their first pointing, participants took twice as long as for the later pointings and latency correlated with the number of intersections to the target, which was not the case for later pointings. These findings are inconsistent with reading out coordinates from a cognitive map but fit well with constructive theories which suggest that participants integrated locations between their current location and the target along the learned path. Later pointings to adjacent intersections within a chunk of trials continued this process using the previous estimation. Additionally, in first pointings participants' estimates were quicker and more accurate when targets were located route forwards than route backwards. This route direction effect shows that the long-term memory employed in generating survey estimates must be directed – either in form of a directed graph or a combination of a directed route layer and an undirected survey layer.

**Keywords:** Spatial memory · Survey knowledge · Environmental space  
Cognitive map · Mental walk · Mental model · Virtual environment

## 1 Introduction

After walking through cities and buildings humans can grasp metric relationships such as distances and directions between remote landmarks. In order to do so they must integrate spatial information obtained across multiple views and places along their navigation trajectory. How do humans store the experienced information and how do they infer survey relations from them when asked to do so?

To solve a survey task, such as pointing to a distant landmark, at least one's current location and the target location must be brought into direct reference. Some theories assume that navigators form a global, world-centered reference frame within which all relevant locations are represented [1–4]. In the following a global world-centered reference frame will be called a cognitive map. Survey relations can be obtained from a

cognitive map by *reading out the coordinates* of the relevant locations (e.g., the current location and the target location) and compute the difference vector between the coordinates to get the relative direction or the distance between the locations, etc. An alternative approach is taken by theories suggesting that a navigable space is not represented within a cognitive map, but by multiple local memory units which are connected in a graph structure [5–7]. For such graph structures Meilinger [7] suggested that for making survey estimates the integration of one’s current position and the target within a single reference frame happens on the fly during retrieval by constructing a *mental model* of the non-visible environment (a related vector-addition model was presented for updating by Fujita et al. [8]). For example, navigators could imagine what the environment would look like if the surrounding walls were transparent. First, they imagine the adjacent street from their current position, then they add the street branching off from it, etc. In this way all locations from the current location along a route leading towards the target location are imagined step by step within the current egocentric reference frame, building a mental model of the environment. No one mentally walks through this constructed environment and the underlying memory structure is no cognitive map, but a graph consisting of local memory units of places interconnected by links.

Increasing evidence for the presence of local memory units can be found in the literature. The use of multiple, locally confined reference frames (one for each corridor) for pointing to distant targets was shown in multi-corridor environments [9–11]. Also, knowledge of spatial relations of targets within a single room seems to be partly dissociated from the knowledge about the location of the room itself [12]. Those studies clearly support graph theories [5–7]. In several studies, longer reaction times were shown for recalling a target location the more local units (e.g., individual corridors) were experienced along the path during learning between one’s current location and the target [11, 13, 14]. In our study we will refer to this effect as the “distance effect”, which should therefore not be understood in its Euclidean sense (i.e., straight line distance), but instead refers to the number of locations visited along a route. Such distance effects can be well explained by a mental model built from a graph-like memory structure [7]. Here, a time consuming, incremental process of activating spatial information along the learned route is underlying the estimation of the relative direction of a target. In contrast, there are other studies supporting the idea of global, cognitive maps, which could be used for a simple read out of coordinates. For example, some studies indicate that participants form reference frames (or reference directions) that are covering multiple local subspaces, such as corridors or streets [9, 11, 15]. They suggest that all spatial information gathered across multiple subspaces have been stored (also) relative to a single reference system in long-term memory. Furthermore, several models allow [6] or propose [16] the combination of local (often route related) and global (typically survey related) memory structures.

Many empirical findings suggest that human spatial memory is directed, or in other words, asymmetric. For example, people occasionally select different routes when either going from A to B compared to going from B to A [17]. Also, the error patterns that are observed when participants estimate the relative direction along a route from location A to location B do not coincide with error patterns when pointing from B to A ([14] same volume). This indicates that no coherent map was underlying survey

performance. Two propositions seem eligible to account for such results. Either, one could argue that two (rather than one) coherent cognitive maps have been built, one for the forward one for the backward direction of the route, which do not need to coincide. No additional information about directed connections between locations need to be stored. Depending on the direction queried (i.e., either from A to B or from B to A), either of the two maps is selected, leading to the observed asymmetries in pointing directions. Alternatively, no global embedding took place, but a graph structure with local memory units that are connected by directed links was stored, for example, a link emphasizing the direction from A to B, but not the other way around [6, 7]. The directed links might render different paths to be preferred for forward and backward route planning and may lead to asymmetric pointing errors as link usage along the link orientation is easier than in opposite direction. For the latter the link must be inverted, which is computationally costly. Support for an embedded directedness in spatial memory comes from studies utilizing primed recognition of landmarks. Re-cognizing landmarks previously experienced along a route is faster when they are preceded by another landmark in the same order as during learning, compared to being preceded by a landmark that was succeeding the target during learning [18–20]. This route direction effect is explained by a directed encoding of connected places in the experienced direction. However, it is unclear whether findings obtained from this simple recognition task generalize to survey tasks as well. Therefore, we aimed to investigate whether directedness is a determinative part of a large-scale space representation utilized in a survey task. To exclude the possibility that navigators formed separate memory structures for route forwards and backward learning (as done by [17] same volume) we had participants learn a route only in one direction.

An interesting aspect not yet addressed in the literature is the question of how transient constructed survey estimations in working memory are and whether subsequent survey estimations can be based on them. Imagine learning landmarks A, B, C, and D along a route and being queried the bearing of D while standing at A in a first trial. Following a construction model, location B and C would be successively activated on the way of mentally walking to or constructing the relative location of D. Now, having pointed to D you are subsequently asked to point to C, the direct neighbor of D. Either this can be done by again constructing a new model from A via B to C. Alternatively, subsequent pointing to C could also be based on the previous estimation of D and calculating backwards from there to derive the location of C. In short, one could use information from the old model to compute subsequent steps from there rather than built a new model from scratch. In that case later pointings should be much quicker than first pointings if neighboring targets are queried, and their latency should not depend on the distance between pointer and target. In our study we set out to examine whether the recall of survey relations is based on all-at-once or incremental processes and whether prior recall of related locations can serve as a base for succeeding targets.

## 1.1 Experiment and Predictions

We had participants learn a virtual route containing a set of to-be-learned locations multiple times from start to end. Subsequently, we administered a survey task where

participants were teleported to different intersections along the route and needed to face straight line direction towards several of the remaining intersections. Hereby, we manipulated multiple factors. We always queried chunks of related locations. Being teleported to an intersection, participants always had to successively recall a sequence of neighboring intersections. This was administered to examine whether later pointing was influenced by prior pointing estimates. Furthermore, targets were always selected relative to participants' current location on the route following two rules: Firstly, we varied whether the targets were lying towards the end of the route (i.e., forward, in route direction) or towards the start of the route (i.e., backwards, against route direction). Secondly, in order to balance the number of intersections between current location and target (i.e., route distance) for first and later pointings within a chunk of related trials, participants were pointing to locations in a target sequence either away from their current location (i.e., first a minimum distance to the adjacent intersection, then the second-next intersection, etc.) or participants pointed in a sequence towards their current location (i.e., first a maximum distance to the start or the end of the route, then to the second/second last intersection, etc., until ending up pointing to the neighboring intersection).

Depending on the underlying memory structure and retrieval process different predictions can be made. An all-at-once read-out process from a cognitive map would neither predict an effect of distance to the target nor an effect of route direction on the performance in the direction estimation task. In contrast, a graph representation accessed via the construction of a mental model assumes a time-consuming incremental retrieval of survey knowledge along the successively visited places towards the target, thus, taking the longer the further the target is away from the navigator along the route (distance effect). Additionally, if the graph representation consists of directed links between adjacent places faster recall of targets located towards the end of the route relative to one's current position should be shown (in learned route direction) compared to estimating direction to targets located towards the start of the route (against route direction). Regarding the interdependence between trials, later pointings within a chunk of trials may re-iterate the whole process and yield identical results as initial pointings. Alternatively, participants may build upon earlier pointing estimates and only add the difference from the previous target to the adjacent intersection. In this case later pointings should be quicker than earlier pointings, show no distance effect and route directions effects might cancel out each other as later pointings depending on the target sequence (towards or away) follow equally often a route upwards and downwards direction.

## 2 Methods

### 2.1 Participants

24 participants took part in the experiment. One participant's performance did not significantly differ from chance and was not included, leading to 23 participants (11 females and 12 males) aged between 21 and 64 ( $M = 29.6$  years,  $SD = 9.3$  years) used in the analysis. All participants were recruited via a subject-database, gave written

informed consent, and were paid for their participation. The procedure was approved by the ethical committee of the University Clinics Tübingen.

## 2.2 Material

**The Virtual City.** In the learning phase, participants had to learn a route through a virtual city. Figure 1 shows a snapshot of the city as seen during walking, as well as a bird's eye view of the route. The route consisted of a start, six intersections and an end, resulting in eight locations that served as targets during testing. During learning, all eight locations were marked with a white X on the floor. The type of houses changed along the route, as did street width and the heights of houses. In addition, individual houses ensured sufficient landmark information to identify each location. The eight locations were not labelled by names.

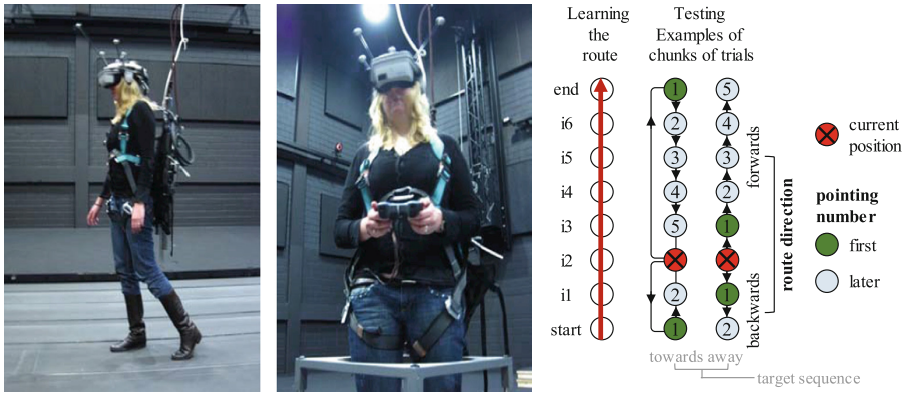
**The Setup.** Participants walked on a  $4 \times 4$  m omnidirectional treadmill (Fig. 2 left side). It allowed them to walk for infinite distances in any direction by moving them back to the center of the treadmill. This unique interface allows for realistic proprioceptive and vestibular feedback as well as efference copies while walking in virtual environments. Participants wore a climbing harness for the unlikely event of falling and hurting themselves on the moving platform. To obtain participants' location on the treadmill we tracked their head position with 16 high-speed motion capture cameras at 120 Hz (Vicon® MX 13). This data was used both to control the treadmill and to update the visualization of the virtual environment. The visual surrounding at a location was rendered in real time (60 Hz) using a NVIDIA Quadro FX 4600 graphics card with 768 MB RAM in a standard PC. Cables connected the PC to the display via the ceiling. Participants viewed the scene in stereo using a nVisor SX60 head-mounted display that provided a field of view of  $44 \times 35^\circ$  at a resolution of  $1280 \times 1024$  pixels for each eye with 100% overlap. The setup thus also provided important visual depth cues such as stereo images and motion parallax. During the test phase a circular handrail around them with 0.48 meters diameter prevented participants from leaving their location (Fig. 2 middle) and responses were given by rotating the head and pressing a button on a gamepad they were holding.

## 2.3 Procedure

In the learning phase, participants walked the route at least six times from start to end. They were instructed to first learn the route, and secondly be able to self-localize when teleported to an X along the route after the learning phase. Participants were free to look around as long as they wanted, however they were not allowed to look or walk back to where they came from. In their first run, they walked up to an intersection, looked around, and the experimenter pointed out the street to take when the participant looked down the correct street by stating "the route is this direction" (the experimenter was in the same room and could talk with the participant). No verbal turning information (e.g., "left", "straight on", etc.) was given. When reaching the end and having looked around participants were teleported back to the start. From the second run onwards participants were asked to approach an intersection, look into the direction the



**Fig. 1.** The virtual city as seen from navigation perspective (left side) and from bird's eye view with the route marked in red (right side). During learning the start, the end and each of the six intersections in-between were marked with white crosses on the floor (marked by red dots in this figure). They served as locations to be teleported to and as targets during the test phase.



**Fig. 2.** Left: participant walking on the omnidirectional treadmill during learning. Middle: participant pointing to a target during testing by facing the target and pressing a button on a gamepad. Right: order of learning and examples of chunks of testing phase. The current position could be at any of the eight locations, *distance* to the targets would vary accordingly. Factors *pointing number* and *route direction* are visualized and that we varied the target sequence. (Color figure online)

route was going on and say “this way”. The experimenter gave feedback whether this was right or wrong, before participants proceeded. They were not allowed to leave the route. For each new run, the virtual environment was rotated 90° clockwise relative to the lab. Sound sources within the lab could thus not be used to derive global orientation. The learning phase ended when participants walked the route at least six times and at least two runs were error-free. This criterion ensured comparable levels of route knowledge for all participants. Participants briefly trained walking on the treadmill before starting the experiment.

In the following test phase, participants were teleported to the eight locations on the route (i.e., the start, the end or i1–i6). The mark (i.e., X) for all locations was removed. For self-localization, participants could look and rotate around, but not walk around. As soon as they subjectively knew their location and orientation, they were asked to press a button on a gamepad. Then they pointed to a chunk of multiple targets. Pointing was done by turning on the spot until a vertical black line in the middle of the display matched the direction in which the participant thought the target was located. Thus, they would look directly at the target location as if the surrounding houses were transparent. When participants thought they faced the target, they pressed a button to confirm the direction and then pointed to the next target. No feedback was provided. After they had pointed to all targets within a chunk, participants pressed a second button on the gamepad and were teleported to a new position.

Figure 2 right, visualizes examples for four chunks of trials participants had to solve. The initial trial within each chunk was labelled “first” trial (dark green in figure), the remaining as “later” trials (light blue in figure), yielding the factor *pointing number*, which was introduced to examine potential dependencies between subsequent survey estimates. Four conditions determined the targets and the order in which participants were asked to point towards them within a chunk of trials. For each chunk they were instructed to point either (1) first to the start and then to all locations between start and their current location in the order of walking (i.e., start, i1, i2, etc.) (lower left example in figure), or (2) they should point to the same locations, but in reverse order (i.e., first the intersection before the current location, then the intersection before that, etc. until finally pointing to the start) (lower right example in figure). (3) They should point to the next intersection along the learned route direction after their current location, then the second next, etc. until pointing to the end (upper right example in figure). Or they should (4) point first to the end, then i6, i5, etc. until pointing to the intersection after their current location (upper left example in figure). Consequently, we varied the *route direction* (backwards to start vs. forwards to end) and target sequence (away vs. towards the current location) within a chunk of trials. *Route direction* served as a factor for analyzing potential directedness in survey estimates. Target sequence was introduced to balance average distance from the current location for first and later targets. Depending on one’s current location along the route the maximum number of intersections one had to point to within a chunk of trials varied. For example, as visualized in Fig. 2 right, standing at i2 facing backwards to the start involves two targets to point to with decreasing or increasing route leg distance across a chunk depending on being queried in towards or away target sequence, while facing forward to the end involves five targets/intersections to point to. Therefore, *distance* in terms of route legs varied across the experimental trials. Please note that the adjacent, neighboring intersections were always visible during pointing.

From the eight locations on the route (including start and end) participants pointed to every other location twice (away and towards their current location). The 28 pointing chunks were presented in random order for each participant (pointing route forwards from seven locations, backwards from seven locations, both in two target sequences). This whole procedure was repeated resulting in 56 pointing chunks. After finishing a chunk participants received feedback on how many targets they missed or how many redundant targets they added. No feedback about pointing accuracy was provided.

Chunks with too few or too many responses were not analyzed as target locations could not be assigned. We recorded self-localization time (not reported), pointing latency and pointing direction for each trial. For the analysis we used latency and computed the absolute pointing error (i.e., the deviation between correct and estimated pointing direction irrespective of the direction of the error). Values deviating more than three standard deviations from the overall mean were not analyzed. Individual pointing accuracy all differed significantly from a random pointing behavior (i.e., 90°), indicating that all participants acquired some survey knowledge.

### 3 Results

To ascertain potential directedness in survey estimates as well as dependencies between subsequent pointings we first conducted a  $2 \times 2$  ANOVA with the factors *pointing number* (first vs. later pointings) and *route direction* (pointing route forwards towards end vs. route backwards towards start). Table 1 summarizes the results for this analysis, Fig. 3 visualizes the performance patterns. Both main factors show a significant effect on latency, *pointing number* also on error. Additionally, both for error and latency, *pointing number* interacted significantly with *route direction*.<sup>1</sup> For first pointings participants pointed quicker ( $t = 4.01$ ,  $p < .001$ ) and more accurately ( $t = 2.11$ ,  $p = .042$ ) when the target was located route forwards towards the end than when located route backwards towards the start. This indicates a route direction effect in survey estimates predicted by directed graph models, but is not expected when reading out coordinates from a cognitive map. Interestingly, no such differences occurred in later pointings ( $t$ 's  $< 1.2$ ,  $p$ 's  $> .23$ ). Participants pointed slower in their first pointing than for later pointings, but also conducted less errors. The effect on latency is consistent with incremental graph theories when assuming that subsequent estimates are based on previous estimates to their direct neighbors.

For the further investigation of a potential incremental process of recalling survey knowledge we additionally considered a correlation analysis, namely, we examined whether latency and error for first and later pointings were associated with the route leg *distance* to the target. Indeed, first pointings showed a *distance* effect on latency. The further away along the route path the target was the longer participants required for pointing as indicated in a positive correlation between distance to the target and latency, with an average correlation of  $r = 0.39$ ,  $SD = 0.29$ , significantly larger than zero,  $t(22) = 6.55$ ,  $p < .001$ . We observed no such correlation for later pointings,  $r = 0.03$ ,  $SD = 0.12$ , difference from zero  $t(22) = 1.03$ ,  $p = .31$ . Errors correlated with distance both for first pointings,  $r = 0.70$ ,  $SD = .14$ ,  $t(22) = 23.8$ ,  $p < .001$ , as well as for later pointings,  $r = 0.45$ ,  $SD = 0.19$ ,  $t(22) = 11.5$ ,  $p < .001$ .

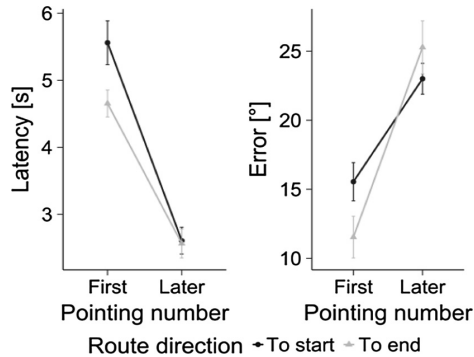
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<sup>1</sup> When including target sequence (albeit not decisive on the introduced models) into the analysis all reported effects remained significant. There was no significant three-way-interaction which could have changed one of the reported effects, and no interaction with route direction. The analysis showed an effect of target sequence and its interaction with pointing number. Here participants were much quicker and accurate when their first pointing was away from their current location towards the visible neighbor intersection.



**Table 1.** Results of the ANOVA for latency and error. Degrees of freedom are  $F(1, 22)$  for each factor(-combination). Significant effects are marked in bold.

	Latency			Error		
	$F$	$p$	$\eta_p^2$	$F$	$p$	$\eta_p^2$
Pointing number	<b>51.23</b>	<b>&lt;.001</b>	<b>.70</b>	<b>34.86</b>	<b>&lt;.001</b>	<b>.61</b>
Route direction	<b>10.04</b>	<b>.004</b>	<b>.31</b>	0.27	.608	.01
Number $\times$ direction	<b>6.50</b>	<b>.018</b>	<b>.23</b>	<b>11.79</b>	<b>.002</b>	<b>.35</b>

**Fig. 3.** Pointing performance in the form of latency (left) and absolute error (right) as a function of route direction and pointing number. Means and within-participants standard errors as estimated from the marginal means are shown.

## 4 Discussion

In our study we aimed to clarify whether survey estimates within navigable space are based on the incremental process of recalling target locations from a graph representation including the successive place-to-place activation of spatial information along the learned path, or whether they are based on an immediate read out of coordinates from an integrated cognitive map. More precisely, in case of reliance on a graph representation we examined whether survey estimates are based on directional encoding in long-term memory and also whether subsequent survey estimates will depend on previous estimates, thus, continuing the incremental process of recalling place-to-place information.

### 4.1 The Route Direction Effect in Survey Knowledge

We found a route direction effect, namely, a difference in performance for first pointing trials depending on whether participants pointed to the start or the end of the route. Participants pointed quicker and more accurate to targets located route forward towards the end of the route compared to pointing route backwards towards the start during the initial trial within a chunk. Such results support graph theories that assume route forwards encoding, as this directed encoding should speed-up integration towards the

end, but slow down integration towards the start. Results for the first pointing are in line with asymmetries observed in spatial memory before in landmark recognition [18–20] and route choice [17] and extend them to survey tasks (see also [14] same volume). They suggest that participants' long-term memory consisted of a directed graph and survey estimates were directly constructed from that graph. Such a directed graph was proposed by Meilinger [7] and the undirected graph-model from Chrastil and Warren [5] is easily adjusted to it. The effect of route direction was not present in later pointings, indicating interdependence of successions of trials discussed further in the following section.

## 4.2 Incremental Integration and Interdependence of Survey Estimates

Contrasting incremental graph theories with simple read-out of coordinates from a cognitive map, only the former predict a route leg distance effect for latency (processing speed) in the first, but not in later pointings of a chunk of trials and interdependence between trials within a chunk (i.e., faster later pointings which profit from earlier pointings). Consistent with incremental theories participants pointed slower in their first pointing than for later pointings, but also conducted less errors. For the first pointing within a chunk participants had to integrate all intersections between the current location and the target. This time took the longer the more intersections were involved as indicated in the positive correlation of latency with route leg distance—an indicator for successive activation of local memory units along the previously learned path, rather than a read out from a cognitive map. Later pointings, successively following neighboring locations of the previous target, showed different patterns. Performance was much quicker on average and did not correlate with the target distance from the participant. This suggests that participants did not repeat the incremental process of integrating all intersections between their current location and the target again, but only added or subtracted the single segment between the old and the new target. Targets for first pointings were on average 2.5 intersections away (averaging towards and away target sequence, where initial pointings for away chunks have a route leg distance of one intersection and where initial pointings for towards chunks can vary between one and seven). In the case of interdependence between trials in a chunk later pointings are always just one intersection away from the previous estimate. Thus, the mean difficulty for estimating the direction to a new target with regards to a distance effect is lower for later pointings compared to first pointings and quicker reaction expected. Alternatively, no new estimate had to be conducted, but instead the target was already present in working memory as part of the constructed mental model and just had to be accessed from there. Neither effect on latency would be expected by read-out from a cognitive map.

For error both in first and later pointings route leg distance correlated with error. This could be due to errors encoded in long-term memory. Assuming a roughly constant random error during encoding, integration across larger distances will aggregate larger errors no matter which process is used. In fact, all models would assume such an effect. In case of integration into a cognitive map, this map would store all locations inside a single reference system, but in a distorted way. In addition to the overall distance effect, error was larger for later pointings. A simple all-at-once read-out from a

cognitive map would not predict such a difference, but incremental models do so. In line with latency results, building upon first estimates, adds up the number of estimates across the chunk of trial. Higher error can be explained by assuming additional error for every mental processing step that is made.

Please note that longer latency for first pointings cannot be explained by additional processing time for self-localization as this happened before pointing. Another aspect is the required head turn. For the first pointing one can expect an average turn of  $90^\circ$  (from a random heading during self-localization to first target). For later pointings, participants only turned towards an adjacent intersection which required a clearly smaller average head turn. We reckon that head movement itself surely is a part of the overall performance but that the observed average latency difference of 2.6 s between first and later estimates encompasses other processes as well. Furthermore, head turning cannot explain the distance effect in our experiment (distant targets do not necessarily require larger head turns – see Fig. 1) and other experiments where no head turning was involved at all and distance effects were still observed [11, 13]. Participants took longer and were more accurate for first pointings, but quicker and more error prone for later pointings. As latency and error correlated within participants on average by  $r = .04$  ( $SD = 0.11$ ), we think that this effect is not simply be due to a speed-accuracy tradeoff.

The fact that the route direction effect disappeared for later pointings further supports the idea that later pointings build upon earlier pointings. If for every target a new incremental construction process was initiated, we should have observed a similar route direction effect as in the first pointings. Subsequent construction from the previous target was equally often along as well as against route direction: as participants pointed in target sequences towards and away from them later pointings always incorporated both route directions and any difference would average out. Therefore, no route direction effect would be expected, just as was observed in our experiment<sup>2</sup>.

### 4.3 Limits and Alternative Explanations

Our results are well explained by forward directed graph models. They account for the observed effects of route direction and distance on error and latency when performing the first trial within a chunk of related trials and can explain the absence of these effects for later trials. However, there are some alternative explanations and considerations that need to be addressed before getting to the conclusion.

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<sup>2</sup> If later estimates were based on estimates of previous targets, the route direction effect for later pointings should invert in the case of towards pointing (see examples in Fig. 2, right). Initially the most distant location must be constructed followed by closer targets, hence, moving along the graph structure in the opposite direction compared to the first target. This inversion for towards pointings is not reflected in participants performance (see footnote 1, no meaningful interactions with target sequence). Thus, the route direction effect does not seem to change in a meaningful way as a function of target sequence. Here participants might have also accessed previously constructed mental model parts still present in working memory. The role of route direction for later pointing thus is not yet fully clear.

The process of recalling survey estimates from a directed graph was described before by Meilinger (see introduction): constructing a mental model of the surrounding non-visible space [7]. Alternatively, navigators could *mentally walk* through a fully integrated cognitive map following the path they walked during learning. While mentally moving from one point to another, they use their path integration system to integrate the metric survey relation between their starting location and their mental position in the map until reaching the target [4, 21], resulting in a homing vector pointing back to their actual, current location. By inverting the resulting vector survey estimates from the location to the target can be derived. The activation pattern of hippocampal place cells is a plausible mediator for this process, although the conscious imagery of the mental walk might take place in posterior parietal cortex. Place cells represent locations within an environment. Even in the absence of sensory stimulation (e.g., during sleep) they can fire in an ordered fashion as they would do when walking a route [22] and such firing patterns were shown even when stationary within an environment [23]. Similar neural processes might happen during mental walks when performing a survey task. Such a mental walk process is also constructive and incremental but not based on a single graph structure.

Importantly, our findings regarding the route direction effect exclude the possibility that pointing relied exclusively on a cognitive map that abstracted from the walked direction, for example, a coordinate system. Assuming a process of mentally walking within a fully integrated cognitive map is not sufficient to explain the observed route direction effect. However, it is possible to account for this effect if survey relations are stored in such a map layer in addition to an asymmetric route knowledge layer [6, 16]. This route layer then must be involved in generating the survey estimates to introduce the observed asymmetries based on the mental walk approach.

Our study extends findings from [14] where participants learned a route in both directions and asymmetries in pointing accuracy were observed. These results could have relied on two separate and differently distorted maps for each walking direction. This is no viable explanation for the result of the present experiment. The learning experience in our study was uni-directional and effects were found both in error and latency. Thus, the asymmetry must be intrinsic to the memory of a single walked direction. Overall, the route direction effect shows that the long-term memory used for pointing must be oriented – either in form of a directed graph or a combination of a directed route layer and an undirected survey layer.

There is an important aspect inherent in the interpretation of our results of route direction as forward encoding, namely, the integration from one's current location towards the target. Such an "away" integration is assumed by both constructive positions, the mental model and the mental walk. However, our data can also be explained otherwise, namely by reversing the assumptions of forward encoding and integration away from the current location into route backward encoding and integration from the target towards the current location. While no theoretic position clearly proposes this possibility, it is still a conceivable alternative explanation that should be considered and discussed. For their first pointing participants might imagine themselves standing at the target location, mentally walk from there towards their current location while updating the vector towards the target. The resulting vector points towards their target. Importantly, to point correctly participants then must align the orientation when

mentally arriving at their current location with their actual, physical orientation at that location as both will differ in most of the cases. For a backwards encoded route this process is quicker and/or more accurately for targets located towards the end (i.e., mentally walking route backwards to the current location) than for targets located towards the start when mentally walking route forwards opposite to encoding. Such a backwards route encoding might be based on spatial updating of previous locations while walking to the next location during learning, thus resulting in vectors pointing backwards. Potentially, navigators then could update not just the last visited intersection, but all previously visited locations as proposed by Wang [24]. For later pointings the previous target vector from current to the first target location first has to be inverted again, the navigator mentally teleported to the old target location which again involves an alignment of the current orientation and the mental orientation taken at the old target. Only then vector updating while mentally walking from the old target to the adjacent novel target can start. While not impossible, the required vector inversions with their associated alignment processes do seem cognitive demanding.<sup>3</sup>

Overall, the reverse model based on the assumption of backwards route direction encoding and integration from the target towards the current location is consistent with our data. Yet, it is disconnected with other theoretic positions, it requires the assumption of cognitive demanding inversion processes, and it is not able to incorporate findings from the literature that clearly support forward encoding. For example, the route direction effect in landmark recognition [18–20]. Furthermore, recognition triggered response models for route knowledge [6, 16] and supporting evidence from route choice [25] also are intrinsically forward oriented. Support for the mental path integration away from ones current location towards the target is given by successive activation of hippocampal place cells along a path to the goal [23]. We think that the easiest explanation and most consistent with the literature is that the route was encoded in walking forward direction and participants integrated from their current location towards the target either by constructing a mental model of the non-visible surrounding [7] or by mentally walking there and using path integration to estimate the resultant vector based on a cognitive map [4, 21] and an additional layer of directed route knowledge.

We are confident that our study provides a reliable basis for our conclusions. Participants learned a highly controlled but realistic city environment and learned from physically walking real life distances on an omnidirectional treadmill involving proprioceptive and vestibular cues. While the sample is not too large (23) it comprises of roughly 50% females and males and spans from 21 to 64 years of age showing a comparatively broad age spread. Furthermore, over 7200 data points went into our analysis which minimizes any random effects. The different comparisons and parameters such as route direction and distance effects across first vs. later pointings nicely correspond and are theoretically and empirically well connected.

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<sup>3</sup> Note that the mental walk model faces similar inversion problems for later pointings. No such inversions are required when pointers construct a mental model of their non-visible surrounding based on a graph representation from their current location towards the target which then is mentally “visible” as an ego-centric vector.

We clearly cannot exclude that direction estimates sometimes relied on strategies rejected here. However, based on the strengths mentioned we think that such strategies can only comprise in a small minority of trials or persons in the present data. For generalization to other situations it is clear that different learning situations can result in different representations and estimation processes such as learning from maps vs. navigation [26, 27]. The reduced visual field and the instruction to not look back towards where participants came from during learning slightly limits generalizability of results as this restriction partly prevents natural navigation behavior. However, support for asymmetries in spatial memory were found in survey estimates despite learning the environment in route-forward and -backward direction [14]. Overall, we believe that our findings apply to real live-experiences when navigators learn a large-scale space exclusively from navigation. Based on our results we cannot exclude the possibility that global integration into a cognitive map and full abstraction from the directedness and incrementality of the learning experience might occur, for example, with extensive exposure to a sufficiently small environment. Nevertheless, one of the main insights from our study remains: to be able to make survey estimates in navigable space it is not necessary to rely on a globally consistent cognitive map. Survey estimates can and seem to be generally based on piecewise spatial knowledge connected by directed links that is used to incrementally recall target locations on the fly.

#### 4.4 Conclusions

The most plausible interpretation of the present results in the light of previous findings and theoretic considerations is that participants encoded the environment route piecewise in route-forward orientation and integrated this information incrementally during survey estimates from their current location towards the first target and from there onwards to later targets. Following the mental model approach, this estimation process relied on a directed graph memory of the space. When extending the mental walk approach, it can likewise explain the results by assuming that the direction estimation is based on a combination of a directed route layer and an undirected survey layer (cognitive map). Importantly, we showed that later pointings depended on earlier pointings. Overall, our results add to the growing evidence that survey estimates obtained via navigation are constructed incrementally during recall and they further show that also survey knowledge is intrinsically oriented.

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