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Abstract

In this study, we examined the extent to which knowledge about the sequence of places encountered during route learning supports the formation of a metric cognitive map. In a between subjects design, participants learned a route until they could navigate it independently without error whilst also learning information about either the identity of places along the route (Recognition Learning condition) or the sequence of places along the route (Sequence Learning condition). In a follow-up Reconstruction of Order Task, we confirmed that participants in the Sequence Learning condition had more accurate route sequence knowledge than those in the Recognition Learning condition, despite requiring the same overall number of trials to learn the route. Participants then completed a Pointing Task to assess the quality of their cognitive map of the environment. Both groups performed above chance level, showing incidental encoding of metric information, but the Sequence Learning group produced significantly lower pointing errors than the Recognition Learning group. Further, we found that route distance between pairs of places was a strong predictor of pointing error in both groups, whilst Euclidean distance between places was a significant, but weak, predictor only for the Sequence Learning condition. The results of this study demonstrate that discrete route sequence knowledge directly supports the formation of metric cognitive maps. We consider how the results are best explained by interactions between striatal route representations and hippocampal metric representations, centered around the sequence of places acting as a scaffold for the encoding of metric information.

KEYWORDS
cognitive map, navigation, route learning, sequence memory

1 | INTRODUCTION

As experience with an environment increases, so does spatial knowledge about routes and places within it. Although different types of spatial knowledge are generally acquired in parallel (Ishikawa & Montello, 2006), the resulting representations vary in terms of their complexity and utility (Chrastil, 2013; Wiener et al., 2009). Coarse discrete knowledge, such as for turning directions or the sequence of places

encountered along a route, is easily attained but offers little behavioral flexibility. In contrast, fine grained metric knowledge embedded into a common coordinate system, often referred to as a cognitive map, contains more precise information about space and affords flexible goal-dependent navigation (Epstein et al., 2017). While there is ample evidence for such an organization of cognitive spatial memory (Chrastil, 2013), little research questions how these different knowledge types that are supported by different networks in the brain, interact and

support each other. We addressed this question by prompting the acquisition of place sequence knowledge during route navigation in participants, who subsequently performed better in a pointing task compared with a control group with less precise sequence knowledge.

Route knowledge is usually defined as discrete representations of specific viewpoint-dependent route information. It includes landmark and place knowledge, place–action pairing, and place sequence knowledge (Hilton, Johnson, et al., 2021). The discrete nature of these components of route knowledge is due to the involvement of associative memory mechanisms providing coarse information about landmark–place relationships ("when I see the town hall, I am at the town center"; Mallot & Lancier, 2018), place–action pairing ("turn left at the town hall"; Waller & Lippa, 2007) and sequence information ("once I pass the town hall, I will arrive at the restaurant"; Strickrodt et al., 2015). Note that sequence knowledge is qualitatively distinct from other types of route knowledge, since it is the only component that pertains to the relationship between different spatial locations.

In a prior study, we reported that participants who had learned and could successfully navigate a route independently showed very high performance on tests of landmark recall and place-action pairing (>90%; Hilton, Johnson, et al., 2021). However, their sequence knowledge was only mediocre (∼50% successfully placed landmarks in a free ordering task). Whilst piecemeal recall of directions at decision points (place–action pairings) without sequence knowledge may be enough to repeat a route, it only provides limited, if any, scope for behavioral flexibility. However, integrating sequence knowledge by combining a place–action pairing with the next encountered place to form place–action–place associations creates a more flexible discrete representation (Trullier et al., 1997). This type of representation allows for the prediction of upcoming places (Schinazi & Epstein, 2010), provides building blocks for the integration of routes to create novel routes (Grzeschik et al., 2021), and allows distinguishing of visually ambiguous locations (such as when landmarks are repeated; Strickrodt et al., 2015). Thus, it can be argued that route sequence knowledge is a crucial aspect of more advanced representations of space that afford more flexible navigation behavior, often referred to as cognitive maps.

Previous studies examined the relationship between cognitive map and route knowledge development. In these studies, participants learned routes before being tested on place, route, and cognitive map knowledge (Anooshian, 1996; Kim & Bock, 2021). Kim and Bock (2021) administered tests of spatial knowledge after every exposure to a route, over a total of 10 exposures. They found that both route and cognitive map knowledge improved gradually over trials, providing support for the parallel acquisition model of spatial learning (c.f., Ishikawa & Montello, 2006). Anooshian (1996) also tested spatial knowledge, after participants had navigated a route whilst learning either the identity of decision-point places, or the turn direction at decision-points during route navigation. Place learning gave rise to place identity, sequence, and cognitive map knowledge, whilst participants in the turn direction learning condition performed poorly on these tasks, and were better at recalling directional information.

Both Anooshian (1996) and Kim and Bock (2021) reported a correlation between sequence knowledge and metric knowledge, but

only when performance on these tasks reached a reasonable level. In the early exposures to the route in the study by Kim and Bock (2021), no relationship between improving route knowledge and cognitive map knowledge was evident. Anooshian (1996) found a correlation between sequence knowledge and metric knowledge only in the place learning group, but not in the turn direction learning group who had less developed sequence and cognitive map knowledge. Anooshian (1996) suggested that dissociations between different knowledge types emerging under certain circumstances highlight the possibility of distinct underlying mechanisms. Building on this interpretation, Kim and Bock (2021) suggested that acquisition of the different knowledge types may start out as relatively independent processes, but gradually converge into overlapping processes as the different information streams become more integrated.

Kim and Bock (2021) assessed overall route knowledge involving both landmark sequence and directional information. Specifically, they combined scores from a landmark sequence test and a directional recall test into one composite score to represent route knowledge. Thus, the observed correlation between route and survey knowledge after the final route exposures in their study was not necessarily specific to only sequence knowledge but also incorporated directional knowledge (possibly explaining the overall weak relationship, $r = \sim.3$). Indeed, Anooshian (1996) tested sequence and directional knowledge in separate tasks and observed a larger correlation between cognitive map and sequence knowledge ($r = \sim.5$), but no correlation with directional knowledge. Overall, prior work provides evidence that acquisition of cognitive map-like metric knowledge is related to sequence learning (Anooshian, 1996; Kim & Bock, 2021). However, these studies only provide circumstantial evidence that the development of sequence knowledge and cognitive map representations pattern together, and not that a causal link exists between them. Kim and Bock (2021) also assessed survey knowledge already during route learning which means that participants could have amended their learning strategies to intentionally acquire both route and survey knowledge.

A mechanistic relationship between sequence learning and cognitive mapping is further supported by an overlap in their neural substrates. Studies of spatial learning strongly implicate the hippocampus as a key brain structure for solving navigation tasks reliant on the cognitive map (King et al., 2002). Other nonspatial memory research implicates the hippocampus in binding of temporal episodes into sequences (Bellmund et al., 2020). This conception of the hippocampus as a key structure in the encoding of memory sequences is not new (Jensen & Lisman, 2005). Yet, in the field of spatial cognition and navigation, sequence learning is a feature of landmark-centered route knowledge that is widely associated with striatal circuits, related to its role in procedural memory (Doeller et al., 2008).

The dichotomy between striatal-base route knowledge and hippocampal-base cognitive map knowledge is prevalent in models of spatial knowledge, and presents an interesting question as to how different knowledge types emerge on a neural level. Goodroe et al. (2018) argued that although routes are typically recalled via strial-dependant stimulus–response associations, the hippocampus also

contributes to route navigation via the input of context-dependent sequence information. Indeed, the striatum and the hippocampus have been shown to interact collaboratively during motor sequence learning (Albouy et al., 2013). Goodroe et al. (2018) posit that the interaction between the striatum and the hippocampus is an important direction for navigation research, which reflects the same question about the relationship between sequence knowledge and metric knowledge on a cognitive level.

For navigation-based sequence learning in rodents, the hippocampus has been shown to be involved in learning sequences of places (Foster & Knierim, 2012), and is recruited during sequence-based navigation, but not during exploration behavior (Babayan et al., 2017). Further, a recent study using human intercranial electroencephalographic recordings showed that neural activity elicited by non-spatial sequence learning closely resembled that predicted by neural models of cognitive map formation, most strongly in the hippocampus (Stiso et al., 2022). In fact, aging adults (both healthy and those showing cognitive decline) often experience marked volumetric decline and structural changes to the hippocampus (Bettio et al., 2017), which coincides with difficulties in spatial sequence learning and cognitive map-reliant navigation in these populations (Lester et al., 2017).

Overall, the independent acquisition of sequence knowledge compared with place and place–action knowledge during route learning (Hilton, Johnson, et al., 2021; Hilton, Wiener, & Johnson, 2021), indicates that sequence knowledge, which involves place-to-place relationships, is distinct from other forms of route knowledge. Further, the correlation between sequence knowledge and cognitive map quality (Anooshian, 1996; Kim & Bock, 2021), the common role of the hippocampus in sequence learning and cognitive mapping, and the overlap in age-related decline (Lester et al., 2017), indicates a possible relationship between discrete route sequence knowledge and metric cognitive map knowledge. Given that (i) most frameworks of spatial learning position sequence learning at a lower hierarchical rank than cognitive mapping (Chrastil, 2013), and that (ii) sequence knowledge tends to reach better levels in navigators before metric knowledge (Kim & Bock, 2021), we propose that route sequence knowledge directly supports the development of a metric cognitive map. Whilst current research only provides circumstantial evidence that cognitive map and sequence knowledge acquisition patterns together, we aimed to determine whether their development is independent, or whether they are interconnected systems.

To test whether route sequence knowledge supports the development of cognitive maps, we asked participants to learn a route and either required them to also learn the sequence of places (Sequence Learning condition), or to learn the identity of the places (i.e., no sequence learning required; Recognition Learning condition). After successful route learning, participants completed a sequence knowledge task to confirm the effectiveness of our manipulation, and then completed a pointing task. The pointing task, where participants were placed at one location in the environment and then pointed directly to another given location, is an established measure of metric spatial knowledge (He et al., 2023), because an understanding of the distances and angles between places is required in order to produce novel pointing vectors between place pairs. Importantly, during route learning participants were naive to the upcoming tasks, and thus could not amend their learning strategies to intentionally acquire metric knowledge. In this way, we tested the incidental development of cognitive maps as a result of enhanced sequence knowledge. We expected participants in the Sequence Learning condition to produce significantly lower angular errors in the pointing task than participants in the Recognition Learning condition. Accepting this hypothesis would support the notion that route sequence knowledge supports cognitive map development. In contrast, rejecting it would suggest that sequence and cognitive map-like knowledge develop independently.

2 | MATERIALS AND METHODS

2.1 | Participants

Forty-one students from Bournemouth University took part in the experiment. Participants were assigned to either the Recognition Learning condition (9 females, mean age = 19.78; 11 males, mean age = 20.18) or the Sequence Learning condition (9 females, mean age = 25.78; 12 males, mean age = 23.33). Ethical approval was granted by the Bournemouth University Research Ethics Panel and written informed consent was gained from all participants who participated in exchange for course credits.

2.2 | Design

Learning condition was the main between groups' independent variable with two levels (Sequence Learning or Recognition Learning). The difference between these two conditions was the alternate task, which participants had to complete during the learning phase. All other parts of the experiment were identical for both conditions. Participants completed in order: the Learning Phase, the Reconstruction of Order Task, and the Pointing Task. Overall, the duration of the experiment varied between 1 and 2 h depending on the time taken to complete the Learning Phase and variations in response times.

2.3 | Virtual environment

We recorded a video of a route through "Virtual Tübingen," a virtual model of Tübingen, Germany (Van Veen et al., 1998). The route consisted of 13 intersections (4 right turns, 5 left turns, and 4 straights; see Figure 1a) and the video was 4 min 49 s long without pauses.

2.4 | Learning phase

Each learning block consisted of one route navigation task and one alternative task (Recognition Learning or Sequence Learning,
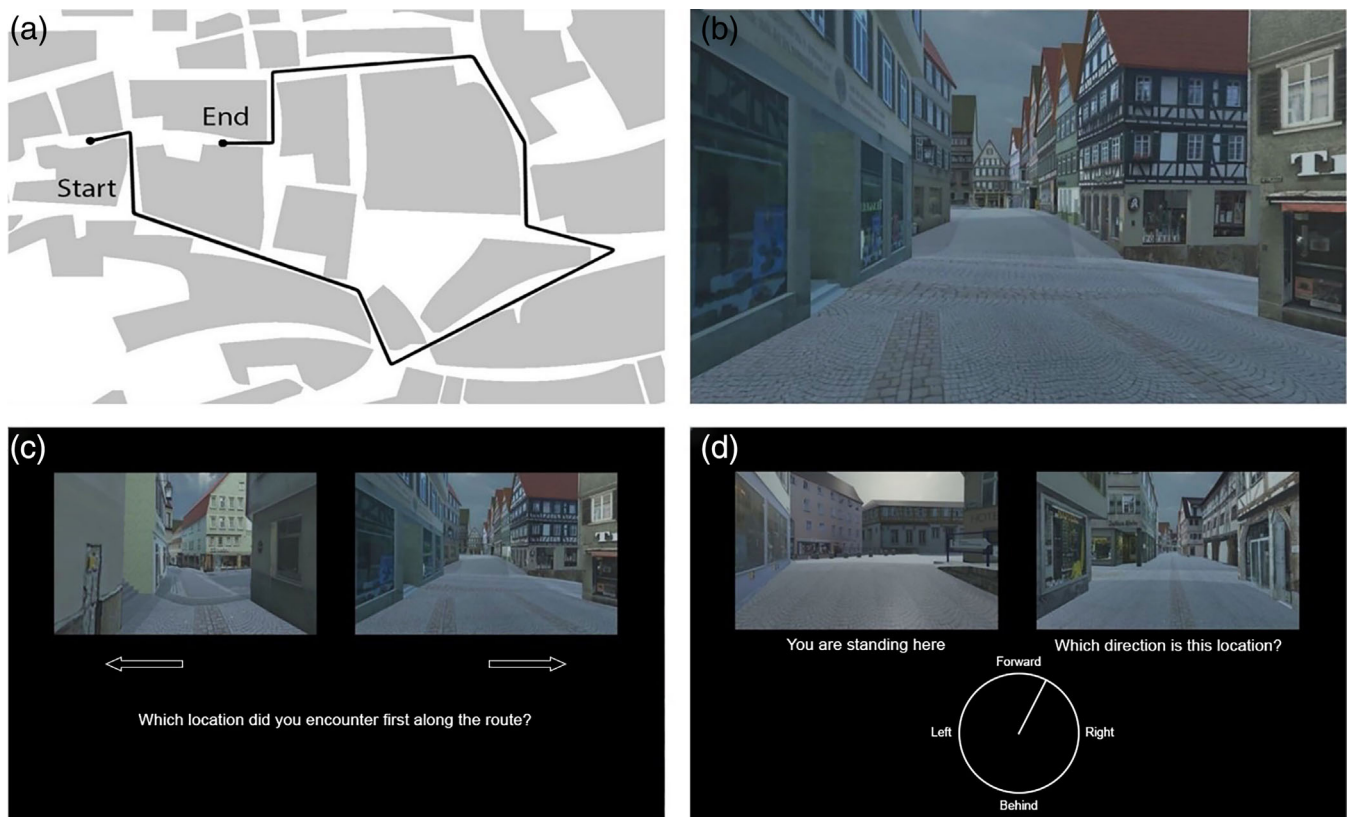
FIGURE 1 (a) Schematic of the route; (b) A screenshot of an intersection in the route; (c) Example trial from the alternate task in the Sequence Learning condition; (d) Example trial from the pointing task.

depending on the condition). Within each block, the tasks were completed sequentially, one after the other, resulting in an interwoven series over repeated blocks (route navigation, alternative task, route navigation, alternative task, etc.). In the route navigation task, participants viewed a video of passive transportation along the route. At each intersection, the video was paused (see Figure 1b), and participants were asked to indicate the direction of travel required to continue along the route via keypresses (left, straight, or right). The video resumed once a response was given, therefore providing participants with immediate feedback. For the first learning block, participants had to guess which directions would be taken since they had never seen the video before. When participants reached the end of the route, they completed the alternative task.

The alternative task depended on which condition participants were in. For the Recognition Learning condition, participants were shown two images of which one was of a location along the route, and one was a foil image taken from a different location in Virtual Tübingen. The task was to indicate which location was encountered along the route. For the Sequence Learning condition, participants were shown two images both of locations from the route, and the task was to indicate which of the locations were encountered first. The two images in the Sequence Learning condition were always of neighboring intersections. Both alternative tasks contained 12 trials in which the side of the screen that correct and incorrect images were presented on was counterbalanced (see Figure 1c).

The learning phase was conducted first and was repeated until participants reached the 100% performance criterion in both the route navigation task and the alternative task in the same learning block, or after eight learning blocks if the performance criterion was not reached.

2.5 | Reconstruction of order task

After the Learning Phase, participants completed the Reconstruction of Order Task, where participants were presented with A4 printed out images of all 13 intersections at once. Their task was to arrange the images into the order in which they were encountered along the route. The task was conducted as described in Ward et al. (2010) in which participants were free to place items in any temporal order they wished and to move items that had already been placed. Participants were given as much time as they needed to construct the sequence and indicated to the experimenter when they were finished.

There were two dependent measures for the Reconstruction of Order Task: first was the absolute scoring method for which each intersection placed in the correct position was scored 1 and each incorrectly placed intersection was scored 0 (c.f. Ward et al., 2010). This measure indicates sequence knowledge in terms of absolute position. It is, however, not sensitive to relative ordering of intersections. For example, imagine a participant places 12 items correctly, and then places the last intersection in position one, thereby

shifting all items one place forward. This would result in a total score of 0, despite having the relative sequence of 12/13 intersections in the correct order. To account for relative positioning, the second measure used was the Levenshtein Distance between the given sequence and the correct sequence (Levenshtein, 1966). The Levenshtein Distance is the number of moves (deletions, insertions, and substitutions) required to transform the given sequence into the correct sequence. Sequences with good relative ordering of intersections have lower Levenshtein Distances than those which have poor relative ordering.

2.6 | Pointing task

The final task was the Pointing Task, for which participants were shown two images of locations from the route simultaneously. Their task was to imagine that they were at the location shown in the left image (indicated on screen) and to point in the direction of the location shown in the right image. Participants were carefully instructed to point as if drawing a direct line between the locations, "as the crow flies," and not pointing in which direction they should turn at the intersection. Participants responded using the mouse to control a line in a circle on the screen (see Figure 1d). They were able to position the pointing line anywhere in the full 360-degree range of the circle. Positioning the line towards the top of the circle represented the participant pointing directly forwards and positioning the line towards the bottom of the circle represented pointing directly behind themselves. Participants clicked the left mouse button to give the pointing response when they had positioned the line.

All combinations of intersections were tested in both directions, for a total of 156 pointing trials. Before the pointing task began, participants were asked to physically point to various locations in the building the experiment took place in (the entrance of the building, the entrance of the testing labs, the nearest staircase) in order to demonstrate their understanding of the pointing task instructions to the experimenter.

2.7 | Materials

OpenSesame 3.1.4 (Mathôt et al., 2012) was used to display stimuli and collect responses. The experiment was presented on a 102 cm screen (diagonal) with an aspect ratio of 16:9 and a resolution of 1920 × 1080 pixels. Participants sat 1 m away from the screen and responded using a standard keyboard.

3 | RESULTS

One participant from the Recognition Learning condition failed to complete the Learning Phase after eight blocks and was excluded from the analysis. Data were analyzed in R studio (RStudio Team, 2021) using the lme4 package for linear and generalised linear mixed effect models (LME; GLME; version 1.1–21; Bates et al., 2015)

and the lmerTest package to determine p-values (Kuznetsova et al., 2017).

3.1 | Learning phase

We analyzed the number of learning blocks taken to reach the 100% performance criterion in the Learning Phase (see Figure 2a). An independent samples t test revealed that there was no significant difference in the number of learning blocks taken to reach criterion between the Recognition Learning condition (mean = 3.74, SD = 1.28) and the Sequence Learning condition (mean = 4.29, SD = 1.15; $t[38] = -1.43$, $p = .161, d = -0.45$).

We conducted a post-hoc power analysis for an independent samples t test using G*Power (v3.1.9.7; Faul et al., 2007). Our study was well powered (0.8) to detect an effect size of at least 0.81, but only achieved a power of 0.4 to observe an effect size of 0.45 (i.e., as reported). It is thus possible that the study was underpowered to detect the numerical difference between groups as significant.

3.2 | Reconstruction of order task

We conducted a GLME on Reconstruction of Order Task absolute scores (binomial) with learning condition as a fixed effect (factor; Recognition Learning or Sequence Learning; sum contrast coding) and random effects of participant and item (intercept only). The model revealed that participants in the Sequence Learning condition (mean = 84.98, SD = 23.52) performed significantly better in the Reconstruction of Order Task than participants in the Recognition Learning condition (mean = 44.94, SD = 25.16; $\beta = 1.69$, SE = 0.37, $z = 4.56$, $p < .001$; see Figure 2b). Similarly, Welch's independent samples t test revealed that Levenshtein Distance was significantly better (i.e., lower) in the Sequence Learning condition (mean = 1.19, SD = 1.72) than in the Recognition Learning condition (mean = 5.63, SD = 2.79; $t[29.37] = 5.98$, $p < .001$, $d = 1.94$; see Figure 2c). To determine chance level performance for this task, we ran a simulation with 1000 iterations of random 13-item sequences compared with the correct sequence. The mean chance level Levenshtein Distance was 11.23. One-sample t tests showed that the Levenshtein Distances in both the Sequence Learning condition ($t[20] = -26.74$, $p < .001$) and the Recognition Learning condition ($t[18] = -8.74$, $p < .001$) were significantly smaller than chance level.

3.3 | Pointing task

Absolute pointing error was analyzed with 0 degrees being perfect pointing accuracy and 180 degrees being the maximum possible error. Using one sample t tests we found that both groups performed significantly better than chance (90 degrees; Recognition Learning: $t[18] = -6.93$, $p < .001$; Sequence Learning: $t[20] = -10.76$, $p < .001$).
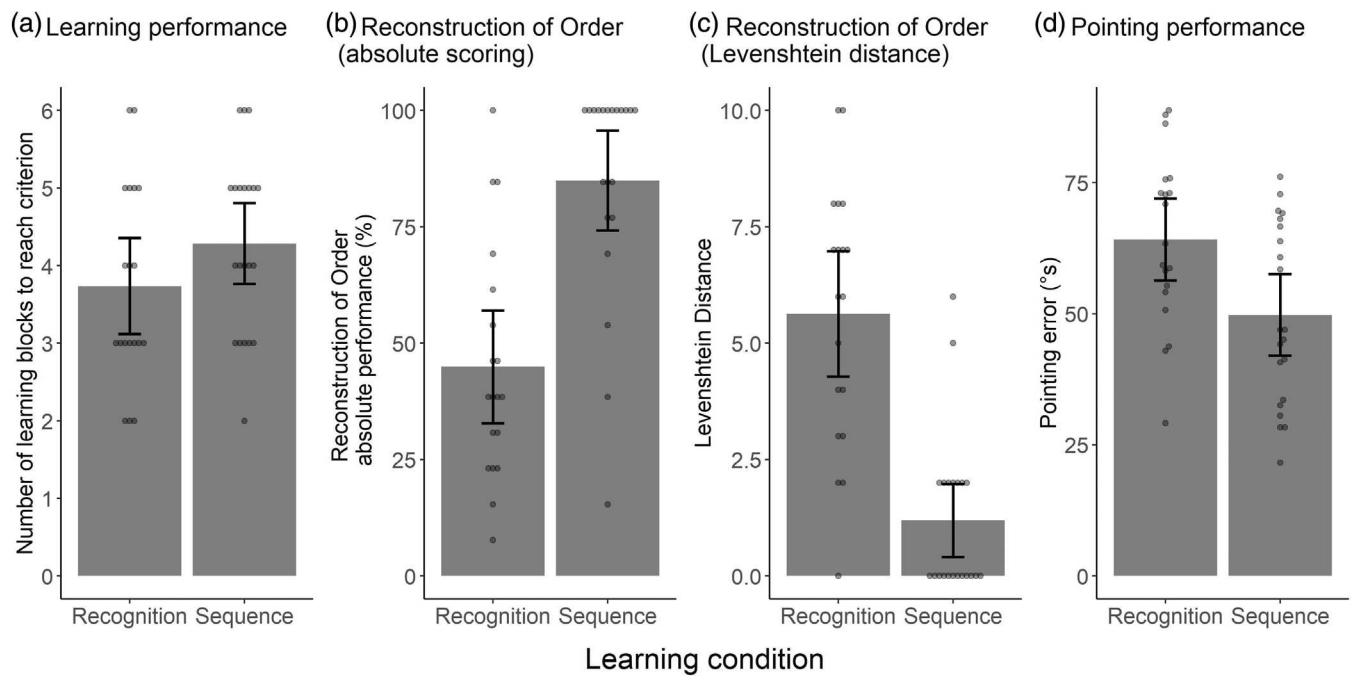
FIGURE 2 (a) Number of trials taken to reach criterion in the Learning Phase; (b) Absolute scoring of the Reconstruction of Order Task; (c) Reconstruction of Order Task Levenshtein's distance between given sequences and the correct sequence; (d) Angular errors on the Pointing Task. Bars represent mean averages, error bars are 95% confidence intervals and points are individual participant data.

We conducted an LME on pointing error with learning condition (factor; Recognition Learning or Sequence Learning; sum contrast coding) as a fixed effect and participant and intersection pair as random factors (intercept only). The model revealed that participants in the Sequence Learning condition (mean = 49.80, SD = 17.13) had significantly lower pointing errors than participants in the Recognition Learning condition (mean = 64.19, SD = 16.24; $\beta = 7.20$, SE = 2.65, $t = 2.72$, $p = .009$; see Figure 2d).

We used the subject and trial variance, and the analysis model structure from this study to run post hoc power simulations using the "simr" package in R (Green & Macleod, 2016). We examined power curves for different sample sizes to detect a large (pointing error = 22.41) and small (pointing error = 10.83) effect size as reported in prior analyses of a pointing task (Weisberg et al., 2014), as well as a medium effect size determined as halfway between small and large (pointing error = 16.62). We ran 1000 iterations per sample and found that total sample sizes of 22, 36, and 72 were required to achieve a power of 0.8 to detect a large, medium, and small effect, respectively.

We also examined the relationship between Levenshtein Distance and pointing errors for the Recognition Learning condition. There was a significant positive correlation between Levenshtein Distance's and pointing errors ($r = .46$, $p = .045$) demonstrating that better sequence knowledge was associated with better metric knowledge. We also checked the relationship between number of learning trials (i.e., total exposure to the route) and pointing errors with a Spearman's rank correlation across all participants and found no significant relationship ($\rho = 0.36$, $p = .134$).

3.4 | Route versus Euclidean distance

We conducted an exploratory analysis into how the distance between place pairs in the pointing task related to performance. For this measure, the distance could be defined by the direct Euclidean distance in virtual units between the places, or by the number of intersections the places were apart along the route, referred to as route distance. There was a significant correlation between the Euclidean and route distance ($\rho = 0.57$, $p < .001$), prohibiting them from being predictors in the same model. This correlation is only of a medium size; however, because places that are close together in route distance will also be close in Euclidean distance, while places close in Euclidean distance are not necessarily close in route distance (e.g., the first and last intersections, see Figure 1a). Therefore, we performed separate models for each measure on pointing error, which included distance as a fixed effect (continuous; either Euclidean or route; centered) and learning condition (factor; Recognition Learning or Sequence Learning; sum contrast coded) and participant and intersection pair as random factors (intercept only). There was a main effect of learning condition in both models as reported in the pointing task analysis above, and thus we do not repeat that here, instead focusing on the distance variables and their interactions with learning condition.

For the route distance model, there was a significant main effect of distance, such that increasing route distance between places related to larger pointing errors ($\beta = 7.80$, SE = 1.11, $t = 7.01$, $p < .001$), and a significant interaction with learning condition ($\beta = -1.94$, SE = 0.55, $t = -3.51$, $p < .001$). We followed up this interaction by running models for each condition

separately, which revealed that route distance was a significant predictor of pointing error for both the Recognition Learning ($\beta = 5.86$, SE $= 1.47$, $t = 3.98$, $p < .001$) and Sequence Learning conditions ($\beta = 9.74$, SE $= 1.11$, $t = 8.80$, $p < .001$), but the slope was greater for the Sequence Learning condition, which explains the interaction.

For the Euclidean distance model, there was no significant effect of distance ($\beta = 0.38$, SE $= 1.28$, $t = 0.30$, $p = .768$), but there was a significant interaction between distance and learning condition ($\beta = -2.30$, SE $= 0.55$, $t = -4.15$, $p < .001$). We followed up this interaction by running models for each condition separately, which revealed that Euclidean distance was a significant predictor of pointing error, with greater distance relating to larger pointing errors, only in the Sequence Learning condition ($\beta = 2.98$, SE $= 1.34$, $t = 2.00$, $p = .047$), while there was no significant effect in the Recognition Learning condition ($\beta = -1.92$, SE $= 1.54$, $t = -1.25$, $p = .213$).

Finally, we compared the Euclidean distance and route distance models in each learning condition to assess which model better fit the pointing error data. The route distance model was a better fit for both the Recognition Learning condition ($\chi2 = 13.62$, $p < .001$) and the Sequence Learning ($\chi2 = 59.26$, $p < .001$) condition.

4 | DISCUSSION

In this study, participants learned a route until they could navigate it without errors whilst also learning either the identity of places along the route, or the discrete sequence in which places were encountered. Not surprisingly, participants who learned the sequence of places performed better on the follow-up Reconstruction of Order Task, confirming that our manipulation to induce route sequence learning worked as intended. Importantly, these participants produced lower errors on the Pointing Task, during which they produced novel pointing vectors between locations along the route, than participants who were not prompted to learn the sequence of places. Overall, the results show that acquiring information about the sequence of places contributes to better understanding of the metric relationships between those places.

As predicted, participants in the Sequence Learning condition performed better on the Pointing Task than participants in the Recognition Learning condition. The Learning Phase results show that this is not likely to be explained by differences in exposure to the route, since no significant difference was observed in this regard. There was a small numerical increase in route attempts for the Sequence Learning groups (0.55 attempts), which we may have missed as a real effect due to insufficient power, but the number of attempts in both learning groups was very similar to that reported by Hilton, Johnson, et al. (2021), four to five attempts on average), where participants learned a route of similar length, but without a secondary task. Additionally, we found that the number of learning attempts across all participants did not relate to pointing error, and thus even if small differences between groups did exist, the number of learning attempts is not a good candidate to explain differences in pointing performance.

Improvement in Pointing Task performance is therefore better explained by the improved route sequence knowledge for the Sequence Learning condition. The Sequence Learning group performed near ceiling level on both absolute and relative measures of the Reconstruction of Order Task. On the other hand, participants in the Recognition Learning group performed similarly to those in other studies testing sequence knowledge (Head & Isom, 2010; Hilton, Wiener, & Johnson, 2021), and still better than chance level. The results demonstrate that incidental sequence learning does occur when initially learning a route but is fairly limited in the absence of an explicit requirement to do so.

Both groups performed above chance level in the pointing task, demonstrating that metric learning occurred in both groups, despite participants not knowing that this type of knowledge would be assessed. Angular errors on the pointing task were fairly high, but were in the range observed by other studies (50–60 degrees; Huffman & Ekstrom, 2019) and in line with the notion that metric cognitive map knowledge accumulates more slowly than discrete route knowledge (Kim & Bock, 2021). Our study shows that simple route learning can give rise to a complex representation of space. Indeed, Anooshian (1996) observed that participants who were prompted to learn place identities performed better on tests of sequence and metric knowledge, which is analogous to the Recognition Learning condition in our study. The control group in Anooshian (1996) learned turning directions only and performed very poorly on the sequence and pointing tasks. Combined with our findings, these results suggest that environmental learning that encompasses multiple types of spatial knowledge depends on the strategy employed during route navigation: basic directional response learning yields very little knowledge, place learning yields some knowledge, and sequence learning results in an even more developed representation.

We observed a correlation between sequence knowledge and pointing performance in the Recognition Learning condition, replicating earlier work showing natural emergence of a correlation between these knowledge types (Anooshian, 1996; Kim & Bock, 2021). By manipulating sequence learning directly, our study reveals a causal link between sequence knowledge and metric knowledge. Whilst the idea that spatial representations transition from discrete landmark sequences to metric cognitive maps is generally well-accepted (Ishikawa & Zhou, 2020), our data suggest that this is an interactive process between the two, rather than independently emerging memory systems (c.f. Kim & Bock, 2021). Importantly, the manipulation used to prompt sequence learning was a purely discrete judgment about which of two neighboring places was encountered first. Yet, performance improved on a pointing task that required metric cognitive map-like knowledge about place-to-place representations for pairs of places that were never prompted in the Sequence Learning task. Therefore, the improvement in pointing performance in the Sequence Learning group was not simply due to additional focus on prompted place pairs, but instead must have arisen from the interaction between sequence learning and another process.

Path integration, the integration of self-motion motion information (from optic flow in stationary desktop navigation), enables

humans to determine the metric distance traveled and angles of turns taken between places (Etienne & Jeffery, 2004). It is possible that knowledge about the order of places provides a scaffold which is integrated with the metric information derived from path integration, for more effective encoding. Indeed, the strong relationship we observed between the route distance separating places and pointing error shows that accumulated metric information was tied to the representation of the route.

The binding of metric information, known to be related to the hippocampal and other medial temporal brain structures (Chrastil et al., 2015; King et al., 2002), to the route representation which is widely associated with striatal circuits, provides several insights into the underlying mechanisms of spatial learning during navigation. Interactivity between the striatum and the hippocampus has already been highlighted as a key factor in spatial learning (Goodroe et al., 2018; Iglói et al., 2010), and such an interaction could explain the results of our study. Specifically, sequence information may be the content of the interaction between striatal route representations and hippocampal metric representations, by which a holistic spatial representation is formed (see also Iglói et al., 2010). Future neuroimaging studies could aim to investigate the interaction between striatal and medial temporal networks during navigation potentially with a focus on place sequence learning.

The notion that route information is input from striatal circuits to the hippocampus to scaffold metric information is also in line with the more general claim in previous work that the hippocampus is involved with route navigation, not just with cognitive mapping (Rondi-Reig et al., 2006). Indeed, Howard et al. (2014) found that the posterior hippocampus tracks route distance to a goal location, which is consistent with our results that metric information is tied to the route configuration. They further found that the anterior hippocampus tracked Euclidean distance to the goal location via input from the entorhinal cortex. In our study, although route distance was the strongest predictor, we also found an emerging relationship between pointing errors and the Euclidean distance separating place pairs for participants in the Sequence Learning condition. This result is consistent with Howard et al.'s (2014) evidence of route- and Euclidean-based encoding structures for metric spatial information.

In their framework of spatial knowledge organization, Chrastil and Warren (2014) proposed that spatial information is first organized in a topological format, reflecting known routes through the environment, which becomes labeled with metric information. As the metric information becomes more precise, a "true" cognitive map that is embedded in a global reference frame forms. Our finding that metric information is bound to the route configuration, possibly via the interaction of striatal and hippocampal representations, is in line with the labeled topology suggested by Chrastil and Warren (2014). The emergence of a coarse Euclidean-based organization for participants in the Sequence Learning condition may be the indicator of the progression to a final map-like representation, which is first aided by the sequence knowledge "scaffold." This progressive integration of metric and route information would account for the findings of prior studies that show that the relationships between cognitive map-like knowledge and route knowledge are not immediately apparent (Anooshian, 1996;

Kim & Bock, 2021), but only arise after an initial route representation is formed, and after which metric information can be integrated (Chrastil & Warren, 2014).

The implications of the findings presented here extend to the investigation of age-related spatial navigation impairments. It is possible that impairments in cognitive map knowledge in older adults (Lester et al., 2017) partially stem from the reduced encoding of route sequence information by older adults (Head & Isom, 2010; Hilton, Wiener, & Johnson, 2021). However, O'Malley et al. (2018) showed that older adults were able to learn landmark sequences of short routes when they were aware about an upcoming sequence knowledge test. Therefore, interventions could aim to train older adults to learn route sequence information as a way to organically improve cognitive map representations. We conducted a pilot test with four older adults using the present experiment. However, the long experiment duration and poor learning performance led us to deem the experiment unsuitable for an older participant sample. In our future research, we intend to reduce the paradigm difficulty by shortening the route and reducing the number of pointing trials to make it suitable for an older adult population. We could then address the question of whether cognitive map representation deficiencies in older adults can be partially ameliorated by prompting the acquisition of sequence knowledge.

In conclusion, results from this study suggest a causal relationship between the acquisition of route sequence knowledge and the development of metric cognitive maps. Focusing navigators on learning the discrete order in which places are encountered along a route so that their sequence knowledge surpasses that which it normally would, improves the incidental acquisition of metric information used to construct a cognitive map. Our findings may provide an insight into the content of the interactions between the host of brain networks recruited during navigation for the formation of advanced spatial representations.

CONFLICT OF INTEREST STATEMENT

The authors have no competing interests to declare.

DATA AVAILABILITY STATEMENT

The datasets and analysis script from this study are available online at the Open Science Framework open access repository: https://osf.io/k56p9/.

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