Exploration patterns shape cognitive map learning

Authors:
Iva K. Brunec1,2, Melissa M. Nantais3, Jennifer E. Sutton3,4, Russell A. Epstein2, Nora S. Newcombe1

1. Temple University
2. University of Pennsylvania
3. University of Western Ontario
4. Brescia University College

Keywords:
Spatial navigation; Cognitive map; Exploration; Virtual reality; Roaming; Environmental structure; Space syntax

Abstract
Spontaneous, volitional spatial exploration is crucial for building up a cognitive map of the environment. However, decades of research have primarily measured the fidelity of cognitive maps after discrete, controlled learning episodes. We know little about how cognitive maps are formed during naturalistic free exploration. Here, we investigated whether exploration trajectories predicted cognitive map accuracy, and how these patterns were shaped by environmental structure. In two experiments, participants freely explored a previously unfamiliar virtual environment. We related their exploration trajectories to a measure of how long they spent in areas with high global environmental connectivity (integration, as assessed by space syntax). In both experiments, we found that participants who spent more time on paths that offered opportunities for integration formed more accurate cognitive maps. Interestingly, we found no support for our pre-registered hypothesis that self-reported trait differences in navigation ability would mediate this relationship. Our findings suggest that exploration patterns predict cognitive map accuracy, even for people who self-report low ability, and highlight the importance of considering both environmental structure and individual variability in formal theory- and model-building.

Acknowledgments
This research was supported by a Discovery grant from the Natural Sciences and Engineering Research Council to J.E.S., National Institutes of Health grant R01 EY031286 to R.A.E., and National Science Foundation grant EHR 1660996 to N.S.N. We thank Sarah Hendricks and Mitchell Decasere for their help with Experiment 2 data collection.
Introduccion

Spontaneous, volitional spatial exploration is a fundamental feature of human and animal behavior (E. Schulz et al., 2019; L. Schulz, 2012; Zurn & Bassett, 2018). Spatial exploration is valuable to an organism because it can facilitate constructing a representation of the spatial structure of the world—a cognitive map—which can then be used to guide goal-directed behaviors such as wayfinding, foraging, and returning to the home base (Calhoun & Hayden, 2015; Davidson & El Hady, 2019; Pfeiffer & Foster, 2013). In the classical formulation, exploration and curiosity are key signatures of a cognitive map. However, the relationship between exploration and cognitive maps is rarely studied, and we know little about how the acquisition of cognitive maps is shaped by different features of exploratory behavior.

Some indirect evidence for a relationship comes from neuroscience. Exploration and active information seeking are particularly prominent drivers of activity in the medial temporal lobes (Gruber & Ranganath, 2019), key brain regions supporting cognitive maps (Bellmund et al., 2018; Epstein et al., 2017; Momennejad, 2020; Peer et al., 2021). Spatial exploration involves active movement, either of the body or the sense organs. In rodents, active foraging and exploration produce stronger hippocampal place cell firing compared to passive transportation (Song et al., 2005), better coding of spatial information in place cells (Terrazas et al., 2005), and stronger grid-like responses in entorhinal cortex (Winter et al., 2015). Visual exploration during spontaneous stop-and-scan events produces place cell firing (Monaco et al., 2014), and visual exploration in both primates and humans evokes entorhinal grid-cell-like representations (Julian et al., 2018; Killian et al., 2012). Exploration also involves decision making, and human neuroimaging studies have shown that hippocampal activity during naturalistic virtual navigation is stronger when active decision-making is required than when it is absent (Howard et al., 2014; Kaplan et al., 2012; Spiers & Maguire, 2006). Together, these data show that active navigation, visual sampling, and decision making—key elements of exploration—induce the activation of neural structures that mediate cognitive maps. This prompts the question of how exploration supports the formation of such maps (Chrastil & Warren, 2012), and how individual differences in exploratory behavior might explain the strikingly variability of the cognitive maps that different navigators can form of the same environment (Furman et al., 2014; Ishikawa & Montello, 2006; Uttal et al., 2013; Weisberg et al., 2014; Weisberg & Newcombe, 2016; Wolbers & Hegarty, 2010).

In the present study, we investigated the relationship between exploration and cognitive maps. Specifically, we extracted moment-to-moment dynamics of behavior as participants explored a new virtual environment, and then related these exploration patterns to the fidelity of the cognitive maps that the participants formed. Our approach contrasts with that used in the typical cognitive map study, in which spatial memories are assessed by contrasting pre-learning and post-learning “snapshots”—a procedure that obscures the rich dynamical process that takes place during real-world learning episodes. We reasoned that if we wanted to understand how exploration allows a navigator to build up a representation of the environment, we needed to unravel the step-by-step process of exploration, the choices people make, where they tend to go, and where they tend to linger.
One aspect of navigational behavior we considered was the extent to which the environment was fully explored. Intuitively, one might consider that an optimal way to explore a novel environment would be to seek out new locations until every possible state in an environment is covered. Variations of this exploration approach have been implemented in machine learning agents (Chentanez et al., 2004; Vezzani et al., 2019), based on the assumption that we are intrinsically motivated to seek out novelty and biased towards visiting previously unseen or less visited spaces. If this is the optimal approach, more accurate spatial memory for a particular environment should stem from higher coverage of the environment. Roaming entropy provides a measure of how many different locations, or states, one visits in a given amount of time (Fig. 3A). Maximal roaming entropy would be achieved by spending equal amounts of time in each environmental location. Rodents reared in enriched environments show higher roaming entropy in new environments and higher hippocampal neurogenesis rates compared to rodents reared in impoverished environments (Freund et al., 2013). Further, humans with higher roaming entropy in their day-to-day GPS traces have stronger hippocampal-striatal connectivity relative to those who explore less (Heller et al., 2020). A recent study also found that patients with Alzheimer’s Disease show significantly reduced entropy compared to healthy older adults (Ghosh et al., 2022). To our knowledge, the inter-individual variability in this measure of exploration has not been linked to the subsequent structure of cognitive maps. A somewhat related measure revealed that participants who showed lower displacement from the start and revisited the same locations more often had less precise memory, relative to those with higher displacement and less revisiting (Gagnon et al., 2018), replicating real world findings (Munion et al., 2019).

Measuring coverage itself, however, is agnostic to environmental structure, even though we know that the geometry of our environments shapes our behavior (Barhorst-Cates et al., 2021; Coutrot et al., 2022) and neural representations (Krupic et al., 2015). Thus, a second issue that we considered is how exploration is shaped by the spatial structure of the environment. This structure can be characterized by space syntax. This set of spatial analysis methods, which were originally developed in architecture, conceptualize the environment as a graph of connected locations (Hillier & Hanson, 1989; Penn, 2003). Previous work has shown that connectivity of individual street segments predicts people’s gaze patterns and mapping ability (Emo, 2014; Pagkratidou et al., 2020), and that human hippocampal activity when virtually navigating through a city neighborhood scales with step-by-step changes in both local and global connectivity of street segments (Javadi et al., 2017). We examine whether the representations that participants form of a virtual campus (Virtual Silcton) are affected by the congruence of their exploration patterns with the spatial syntax of the campus. To do this, we derive a new measure of experienced integration, which describes the extent to which participants concentrate exploration on areas of high global connectivity of each segment to the rest of the environment.

To anticipate our results, in Experiment 1, we found that experienced integration significantly predicted participants’ ability to point between locations and to draw a map of the environment, but roaming entropy did not predict either measure. Thus, participants who visit more
interconnected parts of the environment form better cognitive maps. In Experiment 2, we tested two *preregistered hypotheses* stemming from Experiment 1. First, we hypothesized a replication of the link between experienced integration and cognitive map accuracy. Second, we predicted that experienced integration would mediate the relationship between trait differences in navigational abilities and cognitive map accuracy. We found evidence for the former, but not the latter, hypothesis. These results suggest that environmental structure shapes participants’ cognitive maps, but exploration patterns are not driven by self-reported navigational ability, highlighting the possibility of using directed exploration to construct more accurate cognitive maps.
Methods

Experiment 1

Participants
Data were collected from 84 participants at the University of Western Ontario (31 male). These participants were part of a larger sample of 172 participants, collected for a separate purpose (see Procedure below; Nantais, 2019), and included all participants in the larger sample who had complete navigation logs during exploration. The remaining participants in the larger sample had incomplete navigation logs due to a logging error in the Virtual Silcton software. Participants received course credit or $15. The study was approved by the University of Western Ontario Non-Medical Research Ethics Board.

Virtual Environment
The exploration of Virtual Silcton was implemented in Unity game software (https://unity.com/). The environment was presented to participants using the online Virtual Silcton platform (https://virtualsilcton.com), which automatically synced data to a server. Participants freely moved around the world by using the arrow keys on the keyboard, and could adjust their view by moving the mouse. In contrast to previous implementations of Virtual Silcton (Weisberg et al., 2014; Weisberg & Newcombe, 2016), participants were not guided along any predetermined routes, and were able to leave the paths (i.e., there were no invisible walls in the environment).

Procedure
All participants completed three phases of the experiment: 1) exploration, 2) on-site pointing, and 3) final map drawing. As part of the larger study, each participant was assigned to one of four conditions for the exploration phase: Sketch, Silcton Task, Non-Silcton Task, or Baseline. Participants in all groups were given 16 minutes in total to explore the environment. In the Sketch condition, participants were asked to pause exploring every four minutes and draw a map of the environment for one minute each time. In the Silcton Task condition, participants were again paused every four minutes and were given a checklist of items which included a mixture of landmarks seen in Silcton and foils. The Non-Silcton condition followed the same pattern, except that participants were given a coloring page for 1 minute following each 4-minute interval. Finally, in the Baseline condition, participants continuously explored with no breaks. In the present analyses, we collapsed across the four learning conditions as these were not relevant to our current hypothesis. There were no differences in performance on the pointing task or in Gardony map scores (see below) across these four conditions (Nantais, 2019).

Dataset Subsetting
Out of the full sample of 172 participants, 5 were removed for falling more than 2 standard deviations below the mean in the pointing task, 1 due to experimenter error, and 2 participants for not disclosing their gender. Of the 164 participants remaining after these exclusions, 78 had complete navigation logs. The other participants had complete pointing and map-drawing datasets but due to a technical issue with the Virtual Silcton website, their navigation logs were truncated, meaning that each contained no more than a few minutes of data.
Experiment 2

Participants
We recruited 52 participants to test the preregistered hypotheses (https://osf.io/8dj5x). Participants for this sample were recruited on SONA from the Temple Psychology and the University of Pennsylvania undergraduate research pools. All participants completed the task for credit. The experiment was approved by both university Institutional Review Boards.

Procedure
Participants completed the exploration task on the same online platform as in Experiment 1. Due to the Covid-19 pandemic, we were unable to test participants in person. Instead, participants joined a Zoom call with their camera off and shared their screen. This enabled the experimenter to provide participants with verbal instructions, answer any questions in real-time, and monitor progress throughout the task. The participants’ screens were not recorded during these sessions, but their locations when navigating in the virtual reality environments were logged.

All participants completed three phases: 1) exploration, 2) on-site pointing, and 3) model-building. During exploration, each participant was given 25 minutes to roam the environment freely. They were instructed to attempt to find the 8 named buildings and to remember the names and locations of these buildings. They explored the environment continuously, but they were alerted every 5 minutes to help them keep track of time. The on-site pointing task was the same as in Experiment 1: participants were placed next to each building in the virtual environment and asked to point to every other building. For the model-building task, participants were given a blank rectangle on the screen and bird’s eye view images of all eight buildings. They were instructed to drag and drop the images on the screen in the correct configuration to construct a map of the environment. This task served as a substitute for the drawing of a physical map that was required in Experiment 1. The on-site pointing and model-building tasks were untimed.

We also asked Exp. 2 participants to complete the Perspective-Taking Task (for Adults; Frick et al., 2014) and the Santa Barbara Sense of Direction Task (Hegarty, 2002). These standardized measures of spatial ability were included to test whether the exploration patterns we observed were related to trait differences in navigational ability. Participants filled out the SBSOD questionnaire prior to participating to avoid biasing their responses based on their perceived accuracy in the present task, and completed the PTT-A task at the very end of the experiment. We did not analyze the PTT-A results in the present experiment.

Data preprocessing
Prior to running any analyses, we removed all periods during which participants were stationary for more than 30 seconds from the navigation logs. This approach served to filter out the 1-minute time periods when participants were completing tasks associated with their assigned condition in between periods of exploration in Experiment 1. Pointing scores collected via
virtualsilcton.com in Experiment 1 were corrected using the algorithm described in (Weisberg et al., 2021). Pointing scores in Experiment 2 did not need to be corrected.

Data analysis

To test the relationship between experienced integration and subsequent cognitive map accuracy, we performed linear regression analyses in R (R Core Team). We report standardized beta estimates extracted using the lm.beta package in R (Behrendt, 2014). Effect sizes are expressed as partial eta squared values ($\eta_p^2$) for each predictor (calculated using the effectsize package; Ben-Shachar et al., 2020).

Experienced integration

To relate environmental characteristics to participants’ exploration patterns, we relied on axial integration values previously reported for Virtual Silcton by Pagkratidou et al. (2020). As a summary measure for each participant, we calculated the average integration value of their trajectory (= experienced integration). Participants who spent more time on high-integration segments would therefore have higher experienced integration values than those who spent more time exploring low-integration segments. When deriving this measure, all coordinates more than 10 virtual units away from the path were removed, as no integration value could be assigned to them. As a control covariate, we also calculated the proportion of off-path timepoints out of the total exploration time for each participant.

Roaming entropy

Roaming entropy was calculated as Shannon’s entropy, across 2,500 states in the environment (50 x 50 grid). Roaming entropy is based on the probability of a subject being in a particular state, or location, in a given environment across the entire time period of observation (Freund et al., 2013; Heller et al., 2020).

$$R_{Entropy} = \sum_{j=1}^{n} \left( p_{ij} \times (\log_2 p_{ij}) \right) / \log(n)$$

In this equation, $p_{ij}$ represents the proportion of time across the entire exploration phase that participant $i$ spent in location $j$. The total number of states in the environment (in our case, 2,500), is represented by $n$.

Speed: Mean squared displacement

As an additional measure, we also calculated speed of movement. Speed was expressed as the mean squared displacement (MSD), calculated as the squared value of the displacement at each time-step in any direction, following prior approaches (Gagnon et al., 2018). The step-wise values were then averaged to derive a single value for the entire exploration phase for each participant.

$$MSD = \frac{\sum (j_t - j_{t-1})^2}{n}$$
Cognitive Map Accuracy

In Experiment 1, the accuracy of participants’ cognitive maps was measured in two ways: 1) absolute pointing error in an on-site pointing task and 2) Gardony scores of the maps drawn by the participants. In the pointing task, participants were again placed into the virtual environment in front of each of the buildings. They were asked to point in the direction of every other building by using their cursor to adjust their viewing direction and clicking to record their response. Absolute pointing error is expressed as the average absolute deviation, in degrees, from the correct direction. The Gardony map score was calculated for the participants’ hand-drawn maps of the environment using the Gardony Map Drawing Analyzer software (Gardony et al., 2016). The resulting measure is a correlation ranging from 0 to 1, where 0 would indicate no correspondence between the drawing and the ground truth, and 1 would indicate perfect correspondence. In Experiment 2, we used the same on-site pointing task, but due to the COVID-19 pandemic, we had to conduct the study remotely, so we were unable to collect drawn maps. Instead, we asked the participants to complete a drag-and-drop model-building task where they had to arrange icons of all the buildings on a blank rectangle on their computer screen (Weisberg et al., 2014). The coordinates of the icons were then analyzed using bidimensional regression, and the resulting $R^2$ value (ranging from 0-1) was used as the dependent variable.
Results

We first investigated whether the correspondence between exploration patterns and the graph structure of the environment (experienced integration) predicted cognitive map accuracy. We next compared participants’ performance to three alternative simulated model navigators. Finally, we related each participant’s coverage of the environment (roaming entropy) to their cognitive map accuracy.

Experienced integration

Our hypothesis was that participants who explored areas of high global connectivity would form better cognitive maps. In Experiment 1, higher experienced integration was related to lower absolute pointing error ($\beta = -0.477$, $p < .001$, $\eta^2_p = .234$; Fig. 1C) and more accurate hand-drawn maps ($\beta = .295$, $p = .010$, $\eta^2_p = .09$; Fig. 1C). There was no effect of the proportion of time spent off-path on pointing error ($\beta = .042$, $p = .680$, $\eta^2_p = .002$) or Gardony scores ($\beta = -.044$, $p = .696$, $\eta^2_p = .002$).

In Experiment 2, higher experienced integration again predicted lower absolute pointing error ($\beta = -.347$, $p = .015$, $\eta^2_p = .100$), in line with our pre-registered predictions (Fig. 1D). There was again no significant relationship between pointing accuracy and the time spent off-path ($\beta = .164$, $p = .241$, $\eta^2_p = .030$). Somewhat surprisingly, however, we found no significant relationship between experienced integration and the bidimensional regression $R^2$ value for the drag-and-drop model building task ($\beta = .077$, $p = .589$, $\eta^2_p < .001$; Fig. 1D), and a somewhat weak, but significant relationship between the proportion of time spent off-path and the $R^2$ value ($\beta = -.292$, $p = .044$, $\eta^2_p = .080$).
Figure 1. A) To calculate experienced integration for each participant, we extracted the axial integration values reported by Pagkratidou et al. (2020) for each trajectory and computed their average. The black dot indicates the start location for all participants. B) An example participant's trajectory, color-coded according to the axial integration values, alongside all participants’ color-coded trajectories. C) Variability of experienced integration in Experiment 1 (left) was significantly related to participants’ pointing ability (middle) and to the accuracy of the maps they drew (right). D) Variability of experienced integration in Experiment 2 (left) was significantly related to participants’ pointing ability (middle), not to the accuracy of their drag-and-drop maps (right). Panel B was visualized using matplotlib (Hunter, 2007), and panels C and F were visualized using raincloud plots in R (Allen et al., 2021).

Simulated navigation trajectories

These data show that there is a relationship between exploration patterns and cognitive map formation. One possible driver of this relationship might be strategy: participants who are able to integrate across distal locations in the environment (Fig. 1C-D) might recognize the areas in the environment that are more informative and approach these areas with greater frequency compared to peripheral areas. Such a difference in strategy might be reflected in a tendency to choose paths at decision points that gravitate toward high-connectivity areas. In contrast, less accurate mappers might make choices at decision points that are more random. To formally model this idea, we generated simulated trajectories based on three different possible approaches to exploration: 1) random walk, 2) proportional connectivity bias, and 3) consistent connectivity bias. The code to generate these simulations is available on GitHub (https://github.com/ivabrunec/nav_free_exploration).

Random walk. It is important to consider what random behavior is for a realistic human navigator. The simplest possibility would be to compare participants’ trajectories against Brownian motion patterns, in which they randomly reorient at each step. However, it is unlikely that human navigators, even very bad ones, would exhibit such behavior in a complex, structured environment with clearly defined paths. Instead, to generate ‘human-like random behavior’, we generated simulated trajectories following random walks through the environment expressed as a graph. Random walks were implemented by making a random choice at each decision point, with the constraint that backtracking was prohibited to prevent the navigator from bouncing between pairs of graph nodes.

Proportional connectivity bias. The second approach we implemented was more directed and comprised weighing the options at each decision point based on their subsequent interconnectivity. Under this strategy, a navigator uses memories for local navigational information (e.g. which nodes have more paths) to make choices that will hopefully guide them to areas of higher global connectivity, and thus allow them to build up a better cognitive map. If we take an example of a decision point with two options, path 1 leading to a decision point with three connections would be given a weight of 3, while path 2 leading to a decision point with two

---

1 Note that the precise values will change slightly if the simulation code is re-run, since the generated integration values will differ, as will the sampling in the bootstrapping procedure.
connections would be given a weight of 2. Under a proportional connectivity bias, the simulated navigator picks path 1 60% of the time and path 2 40% of the time (rather than 50/50).

**Consistent connectivity bias.** In our third approach, the simulated navigator was highly biased to choose the path leading to the most interconnected decision point. Weights were determined the same way as in the approach above, but in this case the navigator consistently chose the path leading to the most interconnected node. If there was more than one option with the highest weight, the navigator randomly selected between the maximally-weighted options.

For each of these simulation approaches, we generated 1,000 trajectories for each experiment, which matched the average human trajectories in travel time and distance (see Supplementary Materials). We then calculated the average experienced integration for each of the simulated trajectories in the same way as we did for human participants. To relate the exploration behavior of the simulations to the exploration behavior of the human participants, we split participants into tertiles depending on their performance on the onsite pointing task (Fig. 2A–B). This split was motivated by the notion that navigators in different tertiles might be using different strategies, making it feasible to compare the participants in each tertile to the different simulation approaches rather than comparing all participants to the simulations. We then carried out 1,000 bootstrapped independent-samples t-tests with 1,000 samples each (Canty & Ripley, 2021; Davison & Hinkley, 1997) comparing experienced integration for participants in each of the tertiles against experienced integration for a matched number of randomly sampled simulated trajectories, and calculated the proportion of significant t-tests in each case. A non-significant t-test would indicate that human trajectories in a tertile could not be reliably differentiated from a given simulation approach.

In Experiment 1, human participants had higher integration values than the random walk simulation in 98.7% of comparisons for the top tertile, 86.5% of comparisons for the middle tertile, but only 58.8% of comparisons for the bottom tertile. A similar pattern was observed in Experiment 2, where human integration values were significantly higher than the random walk integration values for 96.2% of comparisons for the top tertile, 96.1% of comparisons for the middle tertile, but only 70.6% of comparisons for the bottom tertile (Fig. 2). These data suggest that while the majority of human participants outperform a random walker, there is a subset of participants (i.e. those in the bottom tertile of mapping performance) whose exploration behavior matches the profile of making a random decision at each decision point.

An even more striking pattern was observed when we compared human participants to the proportional connectivity bias simulations. In Experiment 1, human participants had higher integration values than this simulated walker in 73.5% comparisons for the top tertile, but only 34.7% of comparisons for the middle tertile and 7.7% of comparisons for the bottom tertile. In Experiment 2, the corresponding values were 70.2% for the top tertile, 66.8% for the middle tertile, and 21.4% for the bottom tertile (Fig. 2). Thus integration values for participants with middling-to-poor navigational abilities are consistent with an exploration strategy of gravitating towards more interconnected nodes in the underlying graph, but not doing so consistently.
Finally, we compared human participants to the consistent connectivity bias simulation. In Experiment 1, human participants had higher integration values for only 23.3% of the top tertile comparisons, 4.0% of the middle tertile comparisons, and 0.2% of the bottom tertile comparisons. In Experiment 2, these values were 19.9% for the top tertile, 18.4% for the middle tertile, and 1.8% for the bottom tertile (Fig. 2C). These findings suggest that most human participants, even those with good mapping ability, fail to match the profile of a highly biased navigator who consistently detects and selects the most highly interconnected nodes in the underlying graph of the environment.

Figure 2. A) The integration values for each participant in Experiment 1 split into tertiles according to on-site pointing ability (left); integration values for simulated navigators using different strategies (middle); proportion of 1,000 bootstrapped t-tests for which the human navigators in each tertile perform better than the simulated navigators. B) The same data for Experiment 2.

Together, these data make it plausible that the individual variability that we observed in cognitive maps might reflect the use of different navigational strategies that vary in how successfully they draw navigators to regions of high integration. Are these individual differences in exploration measures driven by trait-level individual differences? Individual differences in navigational ability, measured by the Santa Barbara Sense of Direction scale (Hegarty, 2002) have previously been related to behavioral measures of navigation testing the ability to use cognitive maps. This raises the possibility that they might also relate to the ability to learn new cognitive maps through exploration.
Relationship to self-reported navigational ability

Based on the results of Experiment 1, we preregistered the hypotheses that 1) self-reported navigational ability (SBSOD) should predict pointing ability, and 2) that experienced integration should be a mediator of the relationship between SBSOD and pointing ability. To address hypothesis (1), we fit two multiple regression models, predicting absolute pointing error or the model-building $R^2$ value from experienced integration, SBSOD score, and the time spent off-path.

Experienced integration was a significant predictor of absolute pointing error in the multiple regression ($\beta = -.358$, $p = .010$, $\eta_p^2 = .104$), recapitulating our previous finding from the correlation analysis. SBSOD was also significant, but had an approximately 50% smaller effect size ($\beta = -.272$, $p = .049$, $\eta_p^2 = .051$). The time spent off-path was not a significant predictor ($\beta = .240$, $p = .091$, $\eta_p^2 = .058$). Applying the same model to the bidimensional regression $R^2$ values, we found no significant effect of experienced integration ($\beta = .090$, $p = .502$, $\eta_p^2 < .001$), but there was a significant effect of SBSOD ($\beta = .350$, $p = .012$, $\eta_p^2 = .071$), as well as a significant negative effect of the proportion of time spent off-path ($\beta = -.390$, $p = .007$, $\eta_p^2 = .141$). These data suggest that both experienced integration and SBSOD predicted cognitive map accuracy independently, insofar as cognitive map accuracy is indexed by pointing accuracy.

We next performed a mediation analysis predicting pointing accuracy from SBSOD, with experienced integration as a mediator. The analysis was implemented using the mediation package in R (Tingley et al., 2017), running 1,000 simulations with nonparametric bootstrapping. We found no significant evidence for a mediation effect ($\beta = -.191$, 95% CI [-2.95, 2.24], $p = .856$). We also found no significant evidence for a similar mediation effect on the bidimensional regression $R^2$ from model-building ($\beta = -.191$, 95% CI [-.001, .02], $p = .802$).

Together, these analyses suggest that experienced integration remains predictive of pointing accuracy when accounting for self-reported trait individual differences in navigational ability, but does not mediate the relationship between trait abilities and cognitive map accuracy. This suggests that exploration efficiency may not be captured by self-reported measures of navigational abilities.

Roaming entropy

*Roaming entropy* measures the extent to which a navigator covers the entire environment in their exploration. Despite starting at the same location and being given the same amount of time to navigate, participants showed a range of roaming entropy values. Some participants tended to remain in fewer locations in the environment for a longer period of time, while others covered a greater range in the same amount of time (Fig. 3A).

Roaming entropy was not a significant predictor of pointing error in Experiment 1 ($\beta = -.002$, $p = .986$, $\eta_p^2 < .001$) or Experiment 2 ($\beta = .216$, $p = .125$, $\eta_p^2 = .046$). Nor did it predict Gardony scores in Experiment 1 ($\beta = -.070$, $p = .542$, $\eta_p^2 = .005$; Fig. 3B) or bidimensional $R^2$ values in Experiment 2 ($\beta = -.215$, $p = .126$, $\eta_p^2 = .046$; Fig. 3C). These data suggest that the overall
coverage of the environment is not, by itself, predictive of better cognitive maps. Rather, it is
greater coverage of segments which are more integrated that predicts cognitive map accuracy.

Figure 3. A) Example low and high entropy participants. Roaming entropy was not a significant
predictor of pointing accuracy, hand-drawn map accuracy, or model-building accuracy in B)
Experiment 1 or B) Experiment 2.

Finally, we entered both exploration measures into a single regression model, along with the
proportion of time spent off-path to account for its variability in experienced integration. In
Experiment 1, pointing accuracy was significantly predicted by experienced integration (β =
- .520, p < .001, ηp² = .240), but not roaming entropy (β = -.173, p = .113, ηp² = .028). The
proportion of time spent off-path was also not a significant covariate (β = .083, p = .429, ηp²
= .008). Gardony scores were again significantly predicted by experienced integration (β = .303,
p = .011, ηp² = .091), but not roaming entropy (β = .030, p = .802, ηp² < .001) or the proportion of
time spent off-path (β = -.051, p = .662, ηp² = .003).

In Experiment 2, experienced integration had a somewhat smaller effect size in the overall
model to Experiment 1, and was a marginally significant predictor of pointing accuracy (β =
- .332, p = .052, ηp² = .097). Roaming entropy was again not a significant predictor of pointing
accuracy (β = .031, p = .868, ηp² = .015), nor was the proportion of time spent off-path (β = .146,
p = .412, ηp² = .015). Bidimensional R² values were not significantly predicted by any of the
measures: experienced integration (β = .030, p = .861, ηp² < .001), roaming entropy (β = -.094,
p = .616, ηp² = .054), or time off-path (β = -.236, p = .169, ηp² = .035).
Finally, we wanted to account for the effect of movement speed on these measures. We added movement speed, calculated as the mean displacement over time, to the overall regression models reported above. In Experiment 1, pointing accuracy was significantly predicted by both experienced integration ($\beta = -.393, p < .001, \eta^2_p = .260$) and movement speed ($\beta = -.304, p = .005, \eta^2_p = .102$) when all variables were entered into a single model. As before, roaming entropy and the amount of time spent off-path were not significant (both p-values > .4). Gardony map scores were significantly predicted only by experienced integration ($\beta = .271, p = .036, \eta^2_p = .092$; all other p-values > .5). In Experiment 2, only displacement speed was a significant predictor of pointing accuracy when all of the factors were entered into a single model, suggesting that movement speed may interact with other exploration measures ($\beta = -.321, p = .030, \eta^2_p = .105$). No other measure was significant (all p-values > .3). No measure was significantly predictive of the model-building $R^2$ coefficient: all p-values > .2)
Discussion

In the present study, we investigated how humans explore a previously unfamiliar virtual reality environment and how these exploration patterns affect the accuracy of the cognitive maps that they form. We found that the time spent in highly-interconnected parts of the environment (experienced integration) predicted cognitive map accuracy in two experiments, whereas the overall coverage of the environment (roaming entropy) was not predictive. Interestingly, however, experienced integration did not mediate the relationship between self-reported navigational ability and spatial memory. It is also worth noting that the relationship between individual differences in experienced integration and cognitive mapping was somewhat weaker in Experiment 2. Together, these data illustrate how different exploration patterns give rise to variability in cognitive maps and suggest that the structure of the environment plays an important role in the structure of acquired knowledge.

Spatial navigation and spatial memory experiments in humans typically rely on structured presentation of stimuli which is matched across participants. In everyday life, however, we often actively seek out new information and connections between existing elements of knowledge through exploration – be it in space, social contexts, or existing elements of semantic knowledge (Lydon-Staley et al., 2021). According to some estimates, we consume approximately 34 gigabytes of information in media alone on a daily basis (Bohn & Short, 2012), which is a daunting amount of content to explore, but somehow we are able to seamlessly organize and structure the new knowledge acquired through everyday experience. The present findings suggest that, in the spatial domain at least, this challenge is accomplished in part by the use of intelligent information sampling strategies, and that fine-grained differences in these sampling strategies are reflected in subsequent cognitive maps.

Exploration of spatial and conceptual spaces. Our findings replicate prior work suggesting that higher levels of spatial exploratory behavior relate to more accurate cognitive maps (Farran et al., 2021; Gagnon et al., 2018; Munion et al., 2019). Also mirroring prior results, we found no relationship between exploration measures and self-reported navigational abilities (Gagnon et al., 2018), despite significant relationships between 1) exploration and pointing performance and 2) self-reported spatial abilities and pointing performance. Higher levels of exploration have also been linked to lower spatial anxiety (Gagnon et al., 2016, 2018) and higher well-being in general, as measured by day-to-day experience sampling (Heller et al., 2020). These findings converge on questions to be addressed in future research: are individuals with higher exploration tendencies less anxious in general, and does the tendency to explore in the spatial domain translate to curiosity and information sampling in non-spatial domains? This notion would fit with a previous finding that trait-level curiosity is predictive of knowledge network-building patterns in participants exploring Wikipedia pages (Lydon-Staley et al., 2021). Further, recent work suggests that both spatial and conceptual learning are captured by the same Bayesian generalization model (Wu et al., 2020), but it is unclear whether this would also extend to spatial knowledge acquired by active first-person navigation.

Extracting the structure of the world. The structure of the task at hand and the structure of the environment are important drivers of learning. The nature of connections between bits of
information shapes the speed of learning and nature of representations humans can form (Karuza et al., 2016; Lynn et al., 2020; Qian et al., 2021; Solway et al., 2014). For example, when information is organized as a structured graph, humans tend to pick up on clusters that are closest together on relevant dimension, such as time, space, or semantic distance. Establishing these clusters, or communities, enables us to represent tasks hierarchically and flexibly (Karuza et al., 2016; Solway et al., 2014) as we build structured knowledge by accumulating pieces of information over time (Duncan & Schlichting, 2018; Schapiro et al., 2013, 2016). Simulations and human behavioral experiments suggest that the structure of such information graphs is most useful to us if the communities are tightly clustered into ‘neighborhoods’ of information, highlighting that environments or knowledge structures with different levels of complexity also have different levels of learnability (Karuza et al., 2016; Lynn et al., 2020).

In the spatial domain, the geometry of the environment that one grew up in appears to affect subsequent navigation and spatial learning abilities (Barhorst-Cates et al., 2021; Coutrot et al., 2022). However, it has not yet been systematically tested whether individuals are similarly affected on all new spatial learning or whether there are gradations in strategy flexibility, rather than general ability. Future work will be necessary to determine whether individuals who are successful in a given exploration task would succeed at wayfinding in any new environment, or whether there are systematic interactions between individuals’ ability and environmental structures. A recent investigation of millions of participants suggests that growing up in an environment with a more regular structure impairs the ability to flexibly integrate across locations in new complex environments (Coutrot et al., 2022). Evidence from non-spatial associative structure learning in humans suggests that different stimulus presentation sequences corresponding to different walks through the graph of the task shape the observed behavioral biases (Karuza et al., 2017). Moreover, when participants are able to freely navigate such non-spatial graphs, their planning reflects the underlying hierarchical structure of the task (Balaguer et al., 2016; Solway et al., 2014). These observations dovetail with our present findings which suggest that participants generally showed sensitivity to the connectivity between the nodes in the present environment. However, we also present evidence that there are substantial individual differences in how efficient participants are at extracting such structure, and formal models of learning and exploration should account for these differences.

Interestingly, in the present experiment, the overall coverage of the environment (roaming entropy) was not predictive of cognitive map accuracy, again suggesting that the connectivity of the world was more relevant than the total amount of new territory covered. However, it is important to consider that the environment used in the present study was highly structured, with clearly defined paths. In such environments, the underlying graph properties may be the key factor constraining navigational strategy (Wiener et al., 2004; Wiener & Mallot, 2003). In large-scale open environments, on the other hand, navigational strategies fundamentally shift due to the difference in reference frames (Wolbers & Wiener, 2014), and direction-free displacement measures, such as diffusion or roaming entropy, might capture more navigational variance. Future studies should compare how well different measures capture exploration success in
different environmental structures, and examine whether better navigators are able to adapt their strategy flexibly across these environments.

Our simulation approach suggested that participants’ navigation patterns can be captured by models that use different strategies at decision points. Less accurate mappers’ patterns were more akin to a random walk or a random walk with a slight preference for interconnected nodes. In contrast, the most accurate mappers’ patterns were most akin to a directed walk, preferring to take paths that lead to nodes with highest connectivity values. Importantly, the similarity between human and simulated trajectories suggests that participants were relying on a forward-looking search strategy, as the decision of which path segment to take was reached based on the connectivity value of the subsequent decision point. These data are broadly consistent with the notion that mammals form predictive maps by extracting regularities and structure from the environment (de Cothi et al., 2021; Momennejad, 2020; Stachenfeld et al., 2017). Beyond the convergence with this theoretical viewpoint, our results also highlight the importance of carefully characterizing human navigational behavior when building computational models or artificial agents (Devlin et al., 2021) and for better understanding human exploration tendencies in new environments.

Limitations of the present work. The present study had two key limitations. First, the effects we observed in Experiment 2 were somewhat attenuated relative to Experiment 1. In contrast to Experiment 1, we observed no significant relationship between exploration measures and the $R^2$ value in the model-building task. While there are multiple possible reasons for this discrepancy, it is worth noting that participants were not explicitly told that they would have to draw a map in this study (in contrast to Experiment 1), which may have led them to attend to different aspects of the environment in the navigation phase. Participants were also given more time to explore in Experiment 2 (25 minutes vs. 16 minutes) and each person completed the task on their own personal computer. While we aimed to standardize as many aspects of data collection as possible, these factors may have contributed to different patterns of results. Second, while we observed an otherwise consistent effect of environmental structure on cognitive map accuracy, we did not manipulate it, nor did we direct participants along more vs. less integrated paths. Future studies will be necessary to disentangle the contributions of active navigational decision-making vs. the optimality of the route one experiences in a given environment. For example, it might be the case that simply being guided along inter-connected paths is sufficient for forming an accurate cognitive map. Alternatively, it is possible that less accurate mappers are also less efficient at extracting environmental structure from ongoing experience. This study would also have implications for guidance and signage designed to aid with wayfinding in the real world.

Conclusions. To summarize, this study provides evidence that individual differences in free exploration patterns shape individual differences in cognitive maps. Navigators who prioritized globally interconnected routes formed more accurate maps. Interestingly, however, this effect did not relate to self-reported navigational abilities. Future studies should orthogonally manipulate both the structure of the environment and the optimality of the routes travelled by the participants to disentangle the relative contributions of these factors to cognitive map accuracy.
References


Behrendt, S. (2014). *lm.beta: Add Standardized Regression Coefficients to lm-Objects* (1.5-1) [Computer software].


https://scholar.google.com/citations?view_op=view_citation&hl=en&user=oXuesi4AAAAJ&sortby=pubdate&citation_for_view=oXuesi4AAAAAJ:PR6Y55bgFSsC


https://doi.org/10.1016/j.cognition.2018.06.020


Supplementary Materials
To compare the distance and time captured in human and simulated navigation trajectories, we ran 10,000 t-tests comparing human values against a random sample of 84 (for Experiment 1) or 52 (for Experiment 2) simulated trajectories. In Fig. S1, we plot the distribution of t-values, showing that the vast majority of t-tests fall within non-significant bounds. These data suggest that the simulated trajectories tended to resemble human ones in distance travelled and the amount of time included in each trajectory.

Figure S1. Density curves depicting the t-test values comparing the time and distance of human and simulated trajectories in A) Experiment 1 and B) Experiment 2.