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Evidence for flexible navigation strategies during spatial learning involving path choices

Stephanie Doner[a], Jingyi Zheng[b], Andrew S. McAvan[a], Michael J. Starrett[a], Hannah Campbell[a], Delaney Sanders[a], and Arne Ekstrom[a,c]

[a]Department of Psychology, University of Arizona, 1503 E. University Blvd, 85719, Tucson, AZ, USA; [b]Department of Mathematics and Statistics, Auburn University, Auburn, AL, USA; [c]Evelyn McKnight Brain Institute, University of Arizona, 1503 E. University Blvd, 85719, Tucson, AZ, USA

ABSTRACT

In a classic study in 1946, Tolman et al. found that rodents chose the optimal path to a hidden goal location when given the option to take a shortcut. Subsequent studies, though, found mixed results, including a previous study in humans showing non-optimal response strategies. Here, we tested human participants in a virtual sunburst maze identical to that employed by Tolman. Across three different experiments, we found that participants consistently employed non-optimal response strategies involving either following the encoded route or using the light as a beacon cue. Adding distal boundary cues (Experiment 2) or enhancing idiothetic cues (Experiment 3) led to the same overall results. Our findings suggest participants' search strategies are often suboptimal when given the opportunity to spontaneously take a short cut.

KEYWORDS

Virtual reality; human navigation; starburst maze; omnidirectional treadmill; Tolman replica; navigation strategies

1. Evidence for flexible navigation strategies during spatial learning involving path choices

Shortcuts are often taken as a hallmark of effective spatial navigation. This is because finding the most direct path to a goal when an obstacle prevents navigating on the previous path presumably requires some knowledge of the direction and distance of this goal. Evidence from both rats and humans suggests they choose a direct path to a goal when one of the original paths is blocked (Foo, Warren, Duchon & Tarr, 2005; Hartley, Maguire, Spiers & Burgess, 2003; Iaria, Petrides, Dagher, Pike & Bohbot, 2003; Tolman, 1948; Wood et al., 2018; Javadi et al., 2022; Brown et al., 2020; Widloski and Foster, 2022). They also optimize their paths to take a more direct route over learning when such "short-cuts" are continuously available (Chrastil & Warren, 2013; Morris, Hagan & Rawlins, 1986; Newman et al., 2007; Starrett, Stokes, Huffman, Ferrer & Ekstrom, 2018). There is now increasing evidence, however, that different participants employ different navigation strategies

CONTACT Arne Ekstrom adekstrom@arizona.edu Department of Psychology, University of Arizona, 1503 E. University Blvd, Tucson, AZ, 85719, USA

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(Hegarty, Montello, Richardson, Ishikawa & Lovelace, 2006; Ishikawa & Montello, 2006; Weisberg, Schinazi, Newcombe, Shipley & Epstein, 2014). Accordingly, some participants may be more likely to employ short cuts using a so-called “place strategy” while others may depend more strongly on a so-called “response strategy” in which they use the same route they learned previously (Iaria et al., 2003; Marchette, Bakker & Shelton, 2011; De Cothi et al., 2022). While it is clear that both humans and rats employ short cuts in some situations, the issues we address here are: 1) how consistently different individuals spontaneously perform short cuts, and, 2) under what conditions other cues might bias participant memories for the goal location, resulting in suboptimal shortcuts.

To test whether mammals take short cuts, Tolman et al. developed a paradigm in which rats first learned a single route involving 4 paths with varying lengths and 3 x 90° turns (Tolman, 1948; Tolman, Ritchie & Kalish, 1946). The rat was then presented with 18 different hallways in a “sunburst” configuration to choose from, with the original hallway they navigated during training blocked. Tolman et al. found that the largest proportion of the rats tested (36%) chose hallway 6, which was the most direct path to the reward. This suggested that they had encoded the direction and distance of the goal and retrieved this information to find the optimal path to the goal. The study, therefore, provided evidence for Tolman’s “expectancy” theory, analogous to what is now known as place learning, with the idea being that the physical location (in 2D or 3D) of a goal is learned. Tolman et al. suggested that when animals are trained to follow a route to a particular location, they learn to expect a reward at that specific location based on encoding the direction and distance of the goal (termed “place” or “survey” learning) rather than only retaining a specific sequence of turns on a path, which is termed “response learning.” Place learning is thought to be a more flexible form of navigation because knowing the direction and distance of a location from other locations would, in principle, permit the organism to find it from other locations, thus allowing for the ability to create new routes or shortcuts. Tolman et al. (1946) concluded that rats demonstrated place learning because they were able to select the correct shortcut, which would only be possible if the rats had some knowledge of the location of the goal.

A significant confounding variable in Tolman’s study, however, was the bright overhead light near the goal location, which could have acted as a beacon. This could have made it seem as if the rats knew the location of the food reward but had merely learned to associate the lightbulb with the food reward. We refer to navigating to the light as a “beaconing response” strategy to distinguish it from following the same path as was learned during encoding, which we term a “kinesthetic response” strategy, although the two share some similarities in that both involve some form of a “stimulus-response” sequence. While Tolman countered the idea that his results derived from a response strategy by arguing that landmarks such as the lightbulb are necessary for the animals to orient themselves in the environment, subsequent studies have shown mixed results replicating Tolman's findings without the light and even with the light. A study by Gentry et al. that followed Tolman's procedures and used a bright light near the goal location failed to replicate his results (Gentry, Brown & Kaplan, 1947). Few rats selected the correct shortcut and the majority of them selected paths toward the middle of the apparatus (consistent with a kinesthetic response strategy). This study suggests that, even under conditions identical to those used by Tolman, rats may fail to spontaneously employ short cuts to find reward locations (see also: Grieves & Dudchenko, 2013).

Modifications of Tolman's study design have also failed to provide evidence for rats spontaneously using short cuts and a place strategy. In a two-part study by Birch and Korn, the effects of different lightbulb placements and different training procedures were tested (Birch & Korn, 1958). The conditions involved the light at the same location as Tolman et al.'s (1946) study, on the left side of the environment, or lights illuminated on both sides. In all conditions, Birch and Korn were unable to replicate Tolman's results; they found that their own results changed only slightly when they provided the rats with more training. Overwhelmingly, the rats preferred the path immediately to the left of the blocked off-center path, consistent with a kinesthetic response strategy. Birch and Korn suggested instead a "sensory-integration theory" in which the rats would integrate "kinesthetic" cues like walking the same path and the approaching lightbulb stimulus, most similar to a "hybrid" strategy we outline shortly. Another study by Young et al. found that changing certain aspects of the maze environment changed the results in the Tolman maze as well (Young, Greenberg, Paton & Jane, 1967). When they did not use any visual cues or used blind rats, Young et al. found results largely comparable to Tolman et al. When they added an additional turn at the end of the maze such that there were equal numbers of left and right turns, they found that the tendency to go right toward the food reward was lessened for both rats and squirrel monkeys.

These findings from Young et al. (1967) would appear partially consistent with the idea that animals may employ a variety of strategies when remembering a goal location, in part based on place, kinesthetic response, and beaconing strategies. Overall, the findings from rodents summarized above suggest that whether rats employ short cuts spontaneously may vary somewhat and that the most typical response observed under such conditions with limited training may be one that is either a kinesthetic response (following a similar path) or a beaconing response. A study by Shamash et al. addressed the issue of varying strategies depending on cues by placing a barrier in an open field and determining the effects of removing or changing the dimensions of the barrier (Shamash et al., 2021). If mice employ a place strategy, they should take the most direct route from the start location to the goal location on the other side of the open field. Importantly, though, the routes they take will differ depending on the barrier because the optimal path will depend on the presence and size of the barrier. With the removal of the barrier or when the barrier's shape was altered, Shamash et al. found that mice continued to navigate as if the barrier (or its previous shape) was present, suggesting a combination of kinesthetic, beacon, and place strategies. The authors termed such strategies "hybrid" strategies to indicate situations in which rodents combine different ways of navigating to the goal rather than employing a single one.

Past studies using the Tolman maze in rodents help to generate predictions and models that have been applied to humans, and, somewhat surprisingly, results using the same task in humans have shown somewhat similar mixed results to the subsequent efforts to replicate Tolman et al's findings. Wilson and Wilson tested Tolman's procedures using desktop virtual reality in healthy human participants in which participants saw a first person view of the maze and navigated with a joystick (Wilson & Wilson, 2018). When a light source was placed above the reward location during training and test, they found, similar to the original Tolman et al. study, that the majority of participants chose the correct hallway during test. When the light was shifted −90°or if there was ambient lighting without a visible light source, however, the number of participants choosing the correct hallway dropped somewhat dramatically. In these cases, the majority of participants instead choose a hallway close to the original (blocked) path, consistent with a kinesthetic response strategy. In some cases, participants followed the light, consistent with a beacon response strategy. These findings suggest that human participants, similarly, do not strongly encode the location of the goal and instead may show a bias toward a kinesthetic response.

Wilson & Wilson (2018) study, to the best of our knowledge, is the only study to look at the tendency to employ short cuts with the original Tolman design in humans. There are several important issues raised by the Wilson & Wilson study that we wish to address here. First, because they employed only a dramatic ("big") movement in the light position, it is possible that participants ignored the light altogether during test and therefore fell back on a kinesthetic response strategy, although we note that some participants did indeed show evidence of a beacon response strategy. We address that issue here by including smaller movements of the light (small move one hallway to the right and small move one hallway to the left) to determine whether less perceptible light movements would influence participant's memory for the goal, more consistent with a beacon response strategy. Second, the Wilson & Wilson study involved a relatively modest number of participants (20 participants in each of 3 conditions) and it is possible that with more participants, differences between kinesthetic, beacon, place, and hybrid strategies might be more apparent. Third, a larger sample would be helpful in replicating their

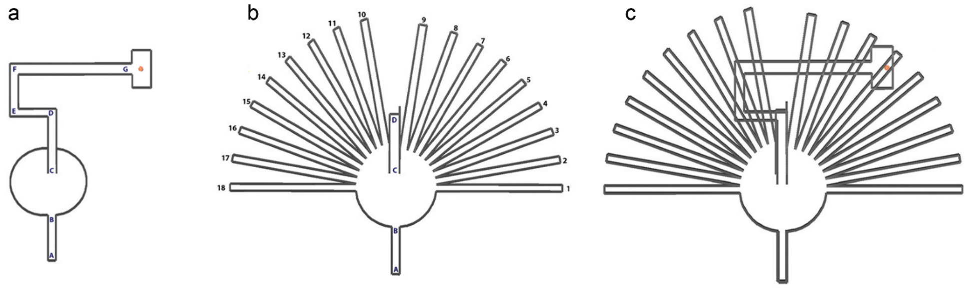

Figure 1. Virtual Environment Images. (a) Overhead view of the Training environment. (b) Overhead view of the Test environment. (c) Training and Test environments superimposed to demonstrate that the goal box from training lines up with hallway 6 from test.

findings to ensure that they generalize. Fourth, the Wilson & Wilson study did not involve allothetic (distal cues such as boundaries) or idiothetic (body-based self-motion) cues, which could have resulted in better encoding of the training path.

We summarize the hypotheses in more detail within the methods and provide them here only briefly. If humans spontaneously employ short cuts under the conditions of the Tolman maze, the place learning hypothesis would predict that the majority of participants would choose hallway 6 as it represents the optimal route to the goal (Figure 1); this should happen regardless of condition and therefore we should not observe an effect of condition in our results. The kinesthetic response hypothesis predicts that the majority of participants reuse the same encoded route from training during test, resulting in the majority of participants choosing a hallway adjacent to the original (blocked) path and therefore no significant difference between conditions. The beacon response hypothesis predicts that the majority of participants follow wherever the light is located during training, predicting a significant effect of condition and a tendency to choose the hallways corresponding to the position of the light. The hybrid strategy hypothesis predicts that participants will employ a mixture of strategies that will depend on combinations of the cues in the environment and some combination of their memory for the position of the goal (place strategy), kinesthetic responses, and beaconing responses.

2. General study design

2.1. Methods

2.1.1. Materials

2.1.1.1. Virtual environment. We created a virtual environment using Unity 3D (Haas, 2014) using custom built VR software, Landmarks (Starrett et al., 2021). The environment was created to have the same layout of Tolman's et al.'s (1946) original study with rodents, with the units converted to virtual meters. The encoding environment (see Figure 1A), termed “Training” in the current study, contained 5 virtual meter tall and 4 virtual meter wide hallways. This environment began with a short 24 virtual meter long hallway (AB) opening up to a circular, 18 virtual meter radius room. Directly across from Hallway AB, exiting the circular room, there was a slightly longer 30 virtual meter hallway, Hallway CD. While this was one continuous hallway, 12 virtual meters were extended into the circular room, and 18 virtual meters continued outside of and away from the circular room. The path turned 90° to the left and continued for 18 virtual meters-Hallway DE. The path then turned 90° to the right and continued for 18 virtual meters, hallway EF. The path then turned 90° to the right and continued for 60 virtual meters as hallway FG, ending in a goal box. In the center of the goal box, there was a strawberry frosted donut that the participant would collide with to end the trial (see Figure 1A).

In the retrieval environment (see Figure 1B), termed “Test” in the current study, hallway AB and the adjacent half of the circular room were identical. The second half of the environment was composed of 19 straight hallways. Each hallway was numbered counter clockwise from 1–18, with the hallway in the center being hallway CD from the training environment. This hallway retained its label from Training, as it was not a possible Test response. Hallway CD also contained a barrier wall at the end, making this path visibly shorter than the others. Hallway CD formed a 90° angle with hallways 1 and 18. Hallways 1 and 18 are 180° apart, with the remaining hallways incremented 10° from each other. Hallways 1–18 are 64 virtual meters long and 4 virtual meters wide.

2.1.1.2. Possible conditions. We created 5 test conditions in which we manipulated the location of the visible light if it was on. The different conditions were ambient lighting; visible light, stable; visible light, big move; visible light, small move right; and visible light, small move left. During Training trials, the light could either be on or off. If the light was on, it was always in the same location 5 virtual meters behind and 10 virtual meters above the goal box (see Figure 2A). The light was not visible in the Ambient condition, and visible for all other conditions. The participant saw a donut at the end of the training maze, within a small rectangular room, the goal box.

In the test trial, the light could be in one of 4 possible locations. The name of the condition refers to the location of the light during the test trial. In the visible light, stable condition, the light was in an identical location over hallway 5. The ambient condition had no obvious light source. In the visible light, big move condition, the light was moved 90° to the left during the test trial to be above hallway 14. In the test trial of the visible light, small move left and right conditions, the light was moved one hallway over Hallways 6 and 4, respectively (see Figure 2B). There was no visible donut in the test trial. At the

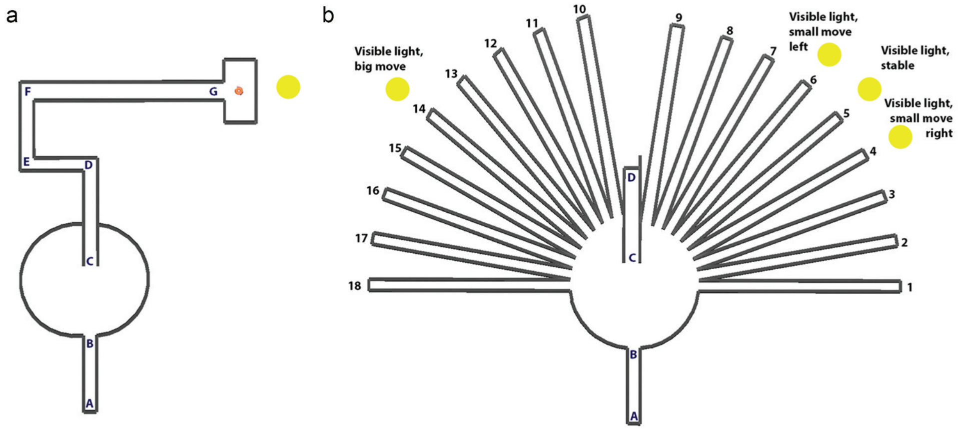

Figure 2. Light locations by Condition. (a) Training Light location-possible light location. (b) Test Light Locations: possible locations of the light based on the condition assigned.

end of hallways 1–18, there was an invisible donut that the participant collided with to signal the end of the trial.

2.1.2. General study procedure

The structure of the trials and blocks of the study were generally identical in each experiment. We highlight any differences below within each experiment's section.

Each block of the study was composed of 7 training trials and 1 test trial with no delay between the trials. The number of training trials was lower than what was typically used with rodents, with the rationale being that the task could be explained to humans and therefore that humans might learn the reward location faster. During training trials, participants were instructed to navigate through the simple maze to the donut in the goal box at the end. Training was repeated for a total of 7 trials. In the Test trial, the participant was instructed that they were in the same room, but aspects had changed. They began the trial in the same location as before, but the original path was now blocked. They were to recall the previous location of the donut as accurately as they could and navigate to that location by using a new path. There was no visible donut in test trials, but subjects were instructed to go to its previous location. Note that the donut remained in the same location on both encoding and test trials, which was at the end of hallway 6 on the test trial, corresponding to the optimal short-cut. This is demonstrated in Figure 1C in which the training and test environments are superimposed. Following this task, online participants of Experiments 1 and 2 completed a navigation survey including the Santa Barbara Sense of Direction (SBSOD) survey (Hegarty, Richardson, Montello, Lovelace & Subbiah, 2002) and a debrief.

2.1.3. General study participants

Participants were recruited from the Tucson, AZ area and from the University of Arizona undergraduate Psychology program. All participants reported normal or corrected-to-normal vision. All studies were approved by the University of Arizona Institutional Board, and informed consent was collected from all participants. All participants were compensated with either course credits (Experiments 1 & 2) or cash (Experiment 3).

2.1.4. General study analysis and statistical methods

We first removed datasets that did not pass our exclusionary criteria. This is commonly done with on-line data sets (Exps. 1–2) due to the inability to monitor participants and ensure their compliance. Previous work has suggested that additional efforts are required to ensure study compliance and data validity when recruiting on-line participants (Aruguete et al., 2019; Holtom, Baruch, Aguinis & Ballinger, 2022). General exclusionary criteria were as follows: (1) Incomplete data set or (2) participant failed the attention check question at the end conclusion of the virtual portion of the study, before the follow-up questions and navigation survey (3) total time in the virtual portion of the study was >2 standard deviations above the mean time. Total time and not total distance was used as an exclusionary criterion. The average time for experiments 1 and 2 was about 10 minutes per block. Excluding based on total time spent in the experiment helped to filter disengaged participants who had stepped away from their computer or were not pressing the keys for to move the avatar for some other reason (e.g., checking e-mail). Inspection of the data suggested that > 2 standard deviations above the mean block time captured individuals who were disengaged from the computer or experiment. We did not employ excessive distance because this could have been due to exploration or wandering.

We calculated participant accuracy by finding the number of correct responses (hallway 6) divided by total responses. We then ran a multinomial log-linear regression model to determine whether condition (independent variable) predicted hallway choice (dependent measure and categorical). We fitted the hallway choice data based on condition to a multinomial log-linear regression model using the visible light – stable condition and hallway 6 as intercepts. We then compared that regression to a null regression using only the intercept of the hallway chosen to get the likelihood ratio test results and a p value from the chi^2 ratios.

Chi square tests were additionally calculated to determine if there were significant dissociation in the responses across the different conditions. A significant chi square test would suggest that the movement of the light had a significant influence on participant choices, which would be more consistent with the beacon or hybrid hypothesis. If participants were using a kinesthetic response or place learning strategy, the Chi Square should show no difference as participants would have selected either hallway 9/10 (kinesthetic response strategy) or 6 (place learning strategy).

Finally, in each experiment we also determined whether the different conditions had an impact on participants' hallway choices by conducting statistical tests to determine whether there were differences by condition. For these statistical tests, we determined that the hallways we were interested in corresponded with light locations during the test trials of the various conditions. In each condition, we compared the number of responses in the hallways that corresponded with the place learning response (Hallway 6), the kinesthetic response (Hallway 10-the hall immediately to the left of the blocked path) and the beacon response strategy (Hallway 4 in the visible light, small move right condition; Hallway 5 in the visible light, light stable condition; Hallway 6 in the visible light, small move left condition; and Hallway 14 in the visible light, big move condition) (see Figure 2). In Experiments 1 &2, comparisons between specific conditions, based on our hypotheses, were conducted using the Fisher's Exact test due to the between-subjects design. In experiment 3, both Chi Square and Fischer Exact tests were substituted with a Bhapkar's Marginal Homogeneity test (Bhapkar, 1966) due to the study being a repeated measures within-subjects design.

We also we calculated average and standard deviation of the participant's Santa Barbara Sense of Direction (SBOD) survey responses and compared the responses of the ambient place and kinesthetic responses to determine if any place learners also had higher scores on the SBOD. To increase statistical power, we pooled data for Experiments 1&2 and therefore these results are reported at the end of Experiment #2.

2.1.5. General study hypotheses

2.1.5.1. Hallway choice distribution hypothesis and predictions.

If participants encode a location for the reward, then their search during the test period should not be evenly distributed. This would be most evident in the Ambient light condition. If the responses were random, then the responses would be equally distributed across all hallways.

2.1.5.2. Place learning hypothesis and predictions.

If participants have an accurate representation of the layout, or even slightly inaccurate mental representation of the training environment, they should choose the most direct path (short cut) to the reward location during test. This is because they should have encoded both the direction and distance of the reward location and therefore should select the most direct path to get there. This would involve ignoring the light and choosing Hallway 6, or hallways close to hallway 6 (e.g., 5,7) in every condition. This hypothesis also predicts that participants do not alter their response in one condition vs. another because the fastest route always (via Hallway 6) remains the same.

2.1.5.3. Kinesthetic response strategy hypothesis and predictions. In rodents, a motor-kinesthetic response strategy would involve repeating the series of learned motor responses learned in training trials. We have adapted this definition to refer to when the human subjects of the current study attempt to employ the same actions learned in training trials to choose a hallway in the test trial. In Experiments 1 and 2, this would involve repeating the same button presses and mouse movements from training trials in the test trial. In Experiment 3, this would involve repeating the same body movements from training trials in the test trial. In all experiments, repeating these actions should lead to the participant choosing a path that is as close as possible to that which was originally encoded. As the original hallway was blocked off, the choices would be the hallways that are the closest to the training path: Hallways 9 or 10.

2.1.5.4. Beacon response hypothesis and predictions. If the participants used the light as a beacon, their responses would follow the test light location regardless of its location during encoding. The median hallway chosen with this strategy would be the light location, which moved depending on the condition.

2.1.5.5. Hybrid response hypothesis and predictions. This hypothesis predicts that participants use a mixture of strategies depending on the condition. For example, participants might choose a hallway somewhere in between the location of the light and correct response, for example. Such strategies may vary somewhat by condition and indicate a tendency to combine different strategies to find the goal.

3. Experiment 1

3.1. Methods

3.1.1. Materials

3.1.1.1. Virtual environment. Experiment 1 was a between-subjects study presented online using desktop Virtual Reality (VR) downloaded onto participants' personal computers.

3.1.1.2. Conditions. Participants were randomly assigned to one of the 5 conditions: ambient lighting; visible light, stable; visible light, big move; visible light, small move right; and visible light, small move left. Each participant completed one block of the study.

3.1.2. Procedure

At the beginning of the study, we collected informed consent and demographic information via Qualtrics (Qualtrics, Provo, UT). Participants then viewed instructions on how to download the study and how to move their first-person point of view avatar within the environment. Participants then downloaded and completed 1 block of the study. Data collected from the study included time in the environment for each trial and hallway choice in each test trial. Follow-up questions included an attention check and participants' confidence in their hallway choice on a 7-point Likert scale. We also asked questions about navigational strategies they may have used and a space to add any other comments they might have. Finally, the online participants completed a navigation survey that included the Santa Barbara Sense of Direction (SBOD) survey (Hegarty et al., 2002) and debrief.

3.1.3. Participants

415 participants consented to participate from the University of Arizona undergraduate Psychology program whose ages ranged from 18 to 52 with a mean age of 19.8. Written consent was obtained before the experiment, and the methods were approved by the Institutional Review Board (IRB) at the University of Arizona.

3.1.4. Analysis

After applying the exclusionary criteria, we were left with a total of 214 usable participant datasets. This includes 43 participants (27 female, 15 male, 1 genderqueer/gender nonconforming) in the ambient light condition, 53 (35 female, 18 male) in the visible light, stable condition, 38 (24 female, 12 male, 1 androgyn, 1 genderqueer/gender nonconforming) in the visible light-big move condition, 40 (30 female, 10 male) in the visible light-small move right condition, and 40 (28 female, 12 male) in the visible light-small move left condition. The differences in number for our different conditions had to do with initially assigning too many participants to the visible light, stable condition. As we had no reason to exclude these participants other than to more closely balance subject numbers, we retained these subjects in our analyses.

The analyses performed were identical to the general study analyses. We calculated overall participant accuracy, ran a multinomial log-linear regression model, a Chi Square test, and conducted Fisher's Exact tests.

Hypotheses. Hypotheses for Experiment 1 are identical to the general study hypotheses.

3.2. Results

415 participants consented to participate. Data was analyzed from 214 Participants (146 female) after applying the exclusionary criteria.

We first considered how accurately participants found the reward location during test in Experiment 1 across all conditions. Only 35 out of 214 participants (16.4%) chose the hallway that would correspond to an accurate shortcut (Hallway 6). This suggests that most participants did not employ an optimal path (short cut) when prompted to remember the reward location. Also of note, 31/214 (14.4%) participants chose a hallway indicating a response strategy (hallway 10). When we also considered hallway 9 to indicate a response strategy, this percent increases to 47/214 (21.69%) of responses

We fitted participant hallway choice based on condition using a multinomial log-linear regression model. Results of the multinomial log-linear regression indicated that we were able to predict which hallway a participant would choose if the condition assigned was known. Coefficients and p values are listed below in Table 1.

We conducted a likelihood ratio test comparing the results our regression model of the hallways chosen by condition to an intercept-only null model. The model that included condition provided a significantly better fit for the data then the null model, with a residual deviance of 939.75 and a likelihood ratio stat of 134.75 ($p < .000005$). This significant p value indicates that condition significantly influenced hallway choice.

A Chi Square test confirmed a significant dissociation across the different conditions in terms of hallway choices ($\chi2(68) = 142.25$, $p < .001$). We then conducted Fisher's Exact test on hallways of interest in different conditions to

Table 1. Experiment 1 – fitted coefficients (p values) from multinomial log linear regression.

Hallway	Visible light, stable – intercept	Ambient Lighting	Visible light, big move	Visible light, small move right	Visible light, small move left
1	−0.846*	0.558*	0.153*	−1.793*	−0.945*
2	−17.282***	15.895***	16.588***	−12.208°	15.490***
3	−15.073***	13.686***	−5.958***	12.434***	13.281***
4	−13.725*	−4.322*	−4.136*	13.283*	11.934*
5	0.357*	−1.051*	−20.287***	−27.043°	−1.456***
7	−1.252*	0.964*	−0.135*	−20.576***	0.847*
8	−0.559*	0.559*	0.271*	−1.387*	−0.134*
9	0.001*	−0.001*	0.810*	−1.253*	0.154*
10	0.001*	1.098*	0.222*	−0.694*	0.405*
11	−0.559*	−0.135*	−19.432**	−2.080*	−1.233*
12	−1.945*	1.657*	0.558*	−18.187***	0.154*
13	−1.946*	−12.027*	0.559*	−19.676***	−14.657***
14	−14.672*	−2.379*	15.231*	−5.064*	−3.193*
15	−1.944*	0.557*	−12.132*	−19.449***	0.152*
16	−15.791***	14.404***	14.404***	13.151***	−8.280***
17	−17.733***	−4.421***	16.346***	−11.088***	15.942***
18	−0.154*	−0.540*	−1.233*	−27.311***	−1.638*

Notes. Reference condition is visible light, stable and reference hallway is 6 (the 'correct' response). AIC value for this model = 1109.752. NA was indicated as a p value when the values that were not able to be calculated due to the hallway not being chosen by participants in this experiment. * $p > 0.05$, ** $0.05 > p > 0.005$, *** $p < 0.005$, °NA determine if hallway choice varied as a function of the light movement. We first focused on whether the presence of the light in the visible light-stable condition resulted in a shift in participant hallways choices for where they thought the reward was located compared to the ambient condition. We ran a 2 × 3 Fisher's exact probability test on Hallways 5, 6, and 10, finding $p < .05$. These findings suggest that the presence of the light had a significant influence on participant hallway selections. As can be seen from Figure 3, this seemed to derive from a switch from a kinesthetic response or place strategy (hallway 10 vs. hallway 6 in the ambient condition) to choosing the location near or under the light (hallway 5 in the light stable condition).

We next compared the light stable and visible light-big move conditions for hallways 5, 6, and 14 in a 2 × 3 Fischer's exact test to determine whether moving the light a large distance influenced participant hallway choices. We again found a significant effect ($p < .00005$) suggesting that the dramatic movement of the light (from hallway 5 during training to hallway 14 at test) did affect participant choices. As can be seen in Figure 3A, more participants chose hallway 14 when the light was there then when it was not, as a result of the light moving from position 5 to position 14.

We next compared the light stable and light small move right conditions, which involved comparing hallways 4, 5, and 6 in a 2 × 3 Fischer's exact test. This allowed us to determine whether small movements of the light between training and test resulted in different choices of where the reward was located compared to the light stable condition. The Fischer's exact test revealed a significant difference across hallways choices ($p < .000005$), suggesting that moving the light a small distance to the right of the location during training

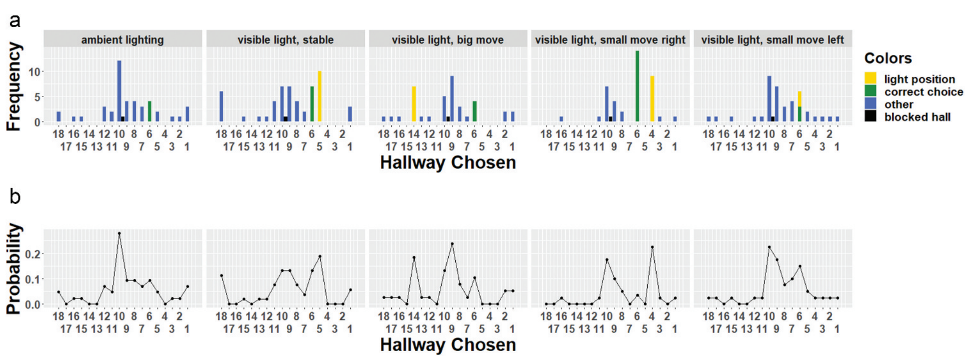

Figure 3. Experiment 1 frequency histogram of hallway choices by condition (top row) and probabilities determined by multinomial regression (bottom row). (A) Frequency histograms that show the number of participants who chose each hallway separated by condition. (B) The probability that the participant will choose a given hallway when the condition assigned is known based on the multinomial regression. Reference condition is visible light, stable and reference hallway is 6.

influenced participant hallway choices compared to keeping the light position stable.

Finally, we did the same analysis for moving the light to the left from training to test, comparing hallways 4, 5, and 6 between the light stable and light move left conditions; this again showed a significant difference with a Fischer's exact test ($p < .00005$). Together, these results suggest that movement of the light significantly influenced participants hallways choices in terms of where they remembered the reward to be.

3.3. Discussion

Overall, participants showed poor memory for the reward location in terms of taking the most direct pathway to get there, with only 16.4% choosing the correct hallway. This suggested that the majority of participants either had an incomplete or noisy representation of the direction and distance of the reward location and/or were influenced by other factors related to the movement of the light. One of the critical conditions here was the Ambient condition which involved only diffuse background light that did not provide a cue to participants to remember the hidden location. As can be seen in Figure 3, the majority of participants in the Ambient condition chose Hallway 10, which would be consistent with a kinesthetic response strategy. Therefore, the majority of participants chose the hallway that was closest in terms of visual angle and turning angle to what they experienced during training (Figure 3A left). These findings largely replicate those reported previously by Wilson & Wilson (2018) (please see Figure 2 from their paper), in which the majority of participants in the ambient condition chose the hallway closest to what they had experienced during training.

Our next question was whether moving the position of the light between training and test would influence participant route choice for the reward locations during test. A multinomial log-linear regression model indicated that when comparing to the light stable condition against all other conditions, there was a clear difference across conditions in terms of participant choices. This is perhaps most clearly demonstrated by the odds ratios, which showed that condition (as an independent variable) predicted significantly different chances of choosing one hallway over (Figure 3B). Somewhat consistent with Wilson & Wilson (2018), we found that moving the light a large distance (from hallway 5 to hallway 14) resulted in a significant number of participants making their choice closer to hallway 14. In particular, we found that even though the light moved a large distance (9 hallways counter-clockwise), participants either searched at hallway 14 or used a kinesthetic response strategy, perhaps deciding that the light was no longer a reliable cue. It is also important to note that hallway 14 was not chosen in any other condition. This indicates that the light's presence over hallway 14 led to it being chosen when otherwise it would not have been. Similarly, when we moved the light a small distance of only one hallway to the right or left of its original location (which would have been above hallway 5) to either hallway 4 or 6, we again found that this significantly influenced participant choices, perhaps more dramatically so. This condition was not run by Wilson & Wilson (2018) and suggests that even small changes in the light movement result in participants changing their hallway choices. The skew to the distributions (toward the correct hallway 6) provides some support for the idea that some subjects also employed hybrid strategies, suggested by choosing intermediate hallways that may have represented combinations of response and place strategies. Overall, however, our findings suggested that the majority of participants employed either kinesthetic or beaconing response strategies, with only a minority employing place or hybrid strategies.

One issue with Experiment 1, however, is the lack of distal cues. It is possible that participants chose to follow the light (or use a response strategy) because they did not have a means to triangulate the position of the reward location relative to distal cues. Therefore, we added an obvious distal boundary with walls of different colors to the environment in Experiment 2. The boundary was always visible to the participants during navigation. Experiment 2 also served to replicate the main conditions of Experiment 1, which included the visible light, stable; ambient; visible light, big move; and visible light, small move right yet under slightly different conditions involving the boundaries.

4. Experiment 2

4.1. Methods

4.1.1. Materials

4.1.1.1. Study design. Experiment 2 was a between-subjects design presented online using desktop VR on participants' personal computers. In Experiment 2, we added distal visual stimuli around the testing environment in the form of brightly colored walls; to provide additional cues, each wall was a different color (see Figure 4). The boundaries could serve as both additional beacons (i.e., a single corner could serve as a beacon) and allothetic cues (the collection of corners and walls would provide a means of triangulation).

4.1.1.2. Conditions. Participants were randomly assigned to one of 4 conditions: ambient lighting; visible light, stable; visible light, big move; and visible light, small move right. The designs of the conditions in this experiment are identical to those in Experiment 1, with the addition of the bright walls of different colors around each environment (see Figure 4). We focused on these

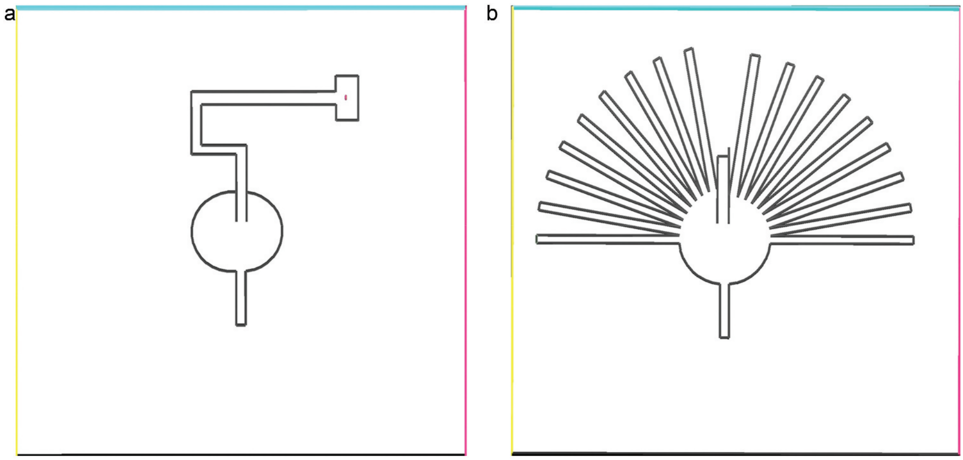

Figure 4. Experiment 2 environment images. Note: this overhead view was not shown to participants during the study. (a) Training environment with distal visual stimuli and visible light. (b) Test environment with distal visual boundaries.

four conditions because light move left was very similar conceptually to light move right (i.e., offset one hallway from the correct location).

4.1.2. Procedure

Procedure for this experiment was identical to Experiment 1.

4.1.3. Participants

265 participants consented to participate from the University of Arizona undergraduate Psychology program. Data was analyzed from 174 Participants (79 female) whose ages ranged from 18 to 32 with a mean age of 19.1 years. Written consent was obtained before the experiment, and the methods were approved by the Institutional Review Board (IRB) at the University of Arizona.

4.1.4. Analysis

Analysis was similar to Experiment 1. We removed datasets that did not pass the general study exclusionary criteria. We then analyzed the data from the remaining 174 participants. This included 43 (31 female, 9 male, 1 androgyn, and 2 genderqueer/gender nonconforming) participants in the visible light-stable condition, 40 (27 females, 9 males, 1 transmale, 3 gender not recorded) in the ambient light condition, 43(24 female, 18 male, 1 not recorded) in the visible light-big move condition, and 45 (32 female, 13 male) in the visible light-small move right condition. Gender information was not recorded for 7 participants as it was lost due to participants not completing the online form correctly. Statistical analyses were identical to Experiment 1.

Hypotheses. The hypotheses are the same as outlined in general methods above and as Experiment 1. For Experiment 2, we additionally hypothesized that the boundary would improve memory for direction and distance, thus resulting in a numerical increase in the number of participants who correctly chose hallway 6 (which led to the goal location) and used a place strategy.

4.2. Results

265 participants consented to participate. Data was analyzed from 173 Participants (79 female) after applying the exclusionary criteria.

We first calculated the overall participant accuracy of Experiment 2 and found that 18/174 (10.3%) of participants chose the hallway corresponding to an accurate shortcut (hallway 6). Again, this suggests that the majority of participants did not spontaneously take accurate short cuts despite the presence of the rich distal cues. We also found that the number of participants who chose a hallway consistent with a kinesthetic response strategy (hallway 10) was 28/174 (16.1%). Including hallway 9 as a possible kinesthetic strategy response, increases this number to 48/174 (27.6%) of individuals.

We next ran a multinomial log-linear regression model to determine if the condition predicted hallway choice. Coefficients and p values are reported in Table 2.

We conducted a likelihood ratio test comparing the results of our regression model of the hallways chosen by condition to an intercept-only null model and found a residual deviance of 803.02 and a likelihood Ratio stat of 79.18

Table 2. Experiment 2-fitted coefficients (p values) from multinomial log linear regression.

Hallway	Visible light, stable – intercept	Ambient Lighting	Visible light, big move	Visible light, small move right
1	−1.098*	1.792*	−14.469***	−0.288*
2	−18.167***	17.474***	−2.717***	−8.750***
3	−16.844***	16.844***	16.151***	15.458***
4	−17.024***	17.429***	17.023***	14.944***
5	0.773*	−0.773*	−0.081*	−2.160**
7	−0.693*	0.693*	1.609*	0.405*
8	−1.098*	2.015*	1.098*	−0.288*
9	−0.405*	1.098*	1.321*	0.272*
10	0.154*	1.099*	1.098*	−0.288*
11	−18.311***	−2.884***	17.617***	−8.856°
12	−18.167***	17.474***	−2.717***	−8.750°
13	−15.832***	−2.608***	−2.462***	13.752***
14	−16.275***	−4.848***	17.527***	14.195***
15	−1.791*	−12.841*	1.098*	−0.288*
16	−0.693*	1.386*	0.692*	−23.076***
17	−1.098*	−16.848***	0.405*	−0.981*
18	−1.791*	2.197*	2.196*	1.321*

Notes. Reference condition is visible light, stable and reference hallway is 6 (the ‘correct’ response). AIC value for this model = 939.0224. NA was indicated as a p value when the values that were not able to be calculated, due to the hallway not being chosen by participants in this experiment. * $p > 0.05$, ** $0.05 > p > 0.005$, *** $p < 0.005$, °NA

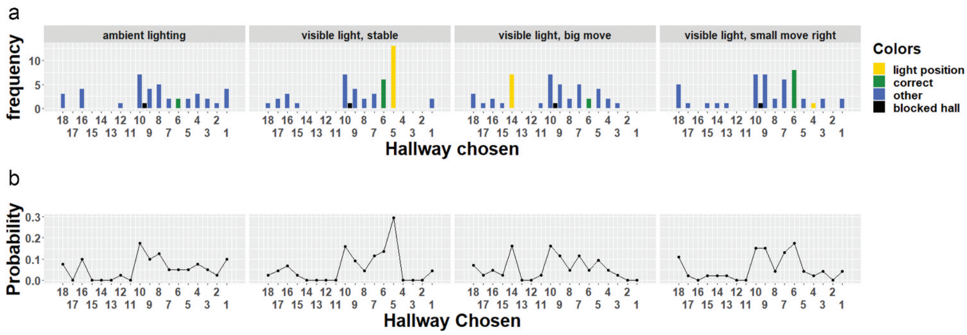

Figure 5. Experiment 2 frequency histogram of hallways chosen by condition (top row) and probabilities determined by multinomial regression (bottom row). (A) Frequency histograms that show the number of participants who chose each hallway separated by condition. (B) The probability that the participant will choose a given hallway when the condition assigned is known based on the multinomial regression. Reference condition is visible light, stable and reference hallway is 6.

Figure 6. The Cyberith omnidirectional treadmill and Vive with HMD and controller used in Exp. 3.

($p < .01$). This significant p value indicates that condition affected hallway choice (Figure 5B).

A Chi Square test confirmed a significant dissociation across the different conditions ($\chi 2(51) = 76.12$, $p < .05$). We then conducted a Fisher's test on hallways of interest in different conditions. We first focused on whether the presence of the light in the visible light, stable condition resulted in a shift in participant hallway choices for where they thought the reward was located compared to the ambient condition. We ran a 2×3 Fisher's exact probability test on Hallways 5, 6, and 10, and it was not significant ($p = .1217$). It is possible that this was due to the fact that a relatively high proportion of participants chose the kinesthetic response hallways (9/10) in the visible light condition. We then used a Fischer 2×3 exact test to compare hallway choices for hallways 4,5,6 to compare light stable and light Small Move-Right conditions; this showed a significant dissociation ($p < .05$), suggesting that participants changed their hallway choice as a result of the light moving to the right. Similarly, comparing light stable and light big move conditions in a 2×3 Fisher's test on hallways of interest 5, 6, and 14, we again found a significant effect of condition on hallways choice ($p < .005$). This again supports the idea that condition (in this case, the light moving between training and test) influenced hallway choice despite the presence of greater allocentric cues.

4.3. Comparing men and women across Experiment 1&2 for place vs. response strategies

Previous studies have reported differences in the tendency of men and women to use place vs. response strategies (Boone, Gong & Hegarty, 2018; Hegarty et al., 2022). As we collected data in the ambient condition in both Experiment 1 and 2, we aggregated data across the two experiments for this condition (we focused on the ambient condition rather than the conditions involving the moving light because the presence of the light induced other choices, (i.e., beaconing)). In the ambient condition there were 56 female participants. 7/56 or 13% of women chose the hallway that corresponded with using a place strategy (i.e., they chose hallway 6), while 19/56 or 34% of female participants chose hallway that indicated a kinesthetic response strategy (either hallway 9 or 10). For the same condition, there was a total of 25 male participants. 3/25 or 12% of men chose the place strategy and 6/25 or 24% chose the response strategy. A Fischer's exact test indicated no significant dissociation of strategy by gender ($\chi 2 = 0.67$, $p > .05$), suggesting no statistically meaningful difference in the tendency of men or women to use one strategy over another.

4.4. Santa barbara sense of direction response analysis

Across both studies, participants in Experiments 1 and 2 had a mean SBSOD score of 3.7 (SD = 1.0). We then filtered the responses to take a closer look at the SBSOD responses from the participants in the ambient lighting condition, who had no influence of a beacon. There was a total of 80 ambient participants. 6/80 or 8% of participants (2 males, 4 females) total chose the 'Place response' hallway (#6) and had an average SBSOD score of 3.2 (SD = 1.6). 27/80 (6 males, 19 females, 1 gender queer/gender nonconforming, 1 transmale) participants had a "kinesthetic response'" hallway choice (Hallways 9 or 10) with an average SBSOD score of 3.7 (SD = 1.0). An independent samples T-Test on the SBSOD scores for all ambient condition participants who executed a "place" or "kinesthetic response" strategy indicated no significant difference in the means $t(31) = -1.0$, $p = .33$. Note that due to our small sample size, we could not further divide by gender for the T-Test analysis.

4.5. Discussion

Numerically, participants performed at a comparable level in Experiment 2 as they did to Experiment 1 in terms of choosing hallway 6 (16% vs. 10%). This suggests that the presence of the boundaries did not improve participant tendency to choose the correct hallway involve using the optimal path (shortcut). The multinomial log-linear regression model, Chi Square test of independence, and Fischer's exact test again showed that condition significantly influenced hallway choice. We also note that again, a significant number of participants employed the response strategy of choosing hallway 10. Together, these findings suggest that participants used beaconing and response strategies to select the hallway with the reward. Experiments 1&2 suggest that a majority of participants spontaneously employ either a beaconing or kinesthetic response strategy. As evidenced by the rightward skew to the probabilities across different conditions (Figure 5), we also found that some number of participants likely used a hybrid strategy involving "averaging" the correct hallway (hallway 6) with hallway 10 (the kinesthetic response choice) and the hallway that the light moved to in the moving light conditions.

There are two potential limitations with Experiments 1&2 we focus on here. First, it may be that participants did not effectively encode the path they followed during training, which involved three 90 degree turns and short and longer hallways. This could be because desktop virtual reality involves reduced idiothetic cues (i.e., walking-based body movements), which could have led to a weaker encoding of direction and distance information. To increase the strength of the encoded path, we added vestibular and other proprioceptive cues (e.g., sensory feedback about body movements) provided by walking on an omnidirectional treadmill. Second, Experiments 1&2 showed that individual participants vary in strategies, which may simply relate to individual differences in navigational strategy (Weisberg et al., 2014). Therefore, to address the second idea, all of the conditions in Experiment #1 were tested here in a within-subject design. If incidental encoding of direction and distance is strengthened with greater access to idiothetic cues, we would expect a greater number of participants to choose the reward location during test; we would also not expect to see a significant effect of condition because the reward location is the same across all conditions (hallway 6).

5. Experiment 3

5.1. Methods

5.1.1. Materials

5.1.1.1. Apparatus. Participants completed this study in immersive VR by using an HTC Vive Head Mounted Display (HMD) and controllers (HTC, New Taipei City, Taiwan), and the Cyberith Virtualizer Elite 2 omnidirectional treadmill (Figure 6). The tasks were run on an ABS Commander (ABS Computer Technologies Inc., Industry, CA) with an NVIDIA GeForce GTX 970 graphics card (NVIDIA Corp., Santa Clara, CA). Participants used a Cyberith Virtualizer omnidirectional treadmill (Cyberith GmbH, Herzogenburg, AT) as the controller of their movement, with head turns rendered through the HMD.

5.1.1.2. Study design. The virtual environments and conditions are identical to the ones used in Experiment 1. Experiment 3, however, involved a within-subjects design in which each participant completed all 5 conditions in a counterbalanced order using a modified Latin-squares design. The first 10 participants saw the conditions in the order of 5 × 5 balanced Latin squares. The last 5 participants viewed the conditions in an order that was randomized and not identical to any of the previous participants. Each block of the study was composed of one condition, with the corresponding 7 training trials and 1 test trial. There was a self-paced break between each trial, and a forced break after each block of the study.

5.1.1.3. Conditions. Each participant completed all 5 conditions: ambient lighting; visible light, stable; visible light, big move; visible light, small move right; and visible light, small move, left.

5.1.2. Procedure

In this experiment, participants completed the task in-person following COVID-19 and VR experience pre-screening. Prior to beginning the study, participants completed informed consent, demographics, a short gaming and VR experience survey, and a simulator sickness questionnaire (Kennedy, Lane, Berbaum & Lilienthal, 1993). Next, participants received a brief verbal overview of the task and instructions of how to walk in the treadmill. We then helped them into the treadmill, fitted the HMD, and gave them one hand-held controller. After ensuring that the participant was as comfortable as possible and that all equipment was functioning, we began the experiment.

Experiment 3 began with 2 practice blocks. In the first practice block, participants completed 4 trials in which they learned to walk in the treadmill and get comfortable with walking to and colliding with targets. In the second block, the participant completed 4 trials in which they practiced walking between the walls in hallways to collide with targets. After the second practice block, they completed a second cybersickness questionnaire to confirm that they were not developing any symptoms.

In the next 5 blocks, the environments were presented as they were in the previous experiments. Each block contained 8 trials – 7 training and 1 test. Participants were offered a self-paced break after every training trial, and a forced break after every test trial. During the forced breaks, participants were offered water and asked the follow-up questions. Following the last follow-up questions, participants were debriefed.

5.1.3. Participants

We recruited 18 participants (10 female, 8 male) from the surrounding Tucson area via a participant database. Participants were paid for their participation. Participants' ages ranged from 18–25 with a mean age of 20.9. Data was analyzed from 15 participants (7 female) based on the exclusion criteria described above. All participants had normal or corrected-to-normal vision, normal or corrected-to-normal hearing, and reported no history of cardiovascular problems or motion sickness. Written consent was obtained before the experiment, and the methods were approved by the Institutional Review Board (IRB) at the University of Arizona.

5.1.4. Analysis

Three datasets were excluded because the participants withdrew from the study from early signs of cybersickness or otherwise feeling uncomfortable with using VR. We then considered the remaining participant responses (hallways chosen) during the test trials and used this data to determine overall experiment accuracy. To determine whether the different conditions had an impact on their choices, we conducted statistical tests to determine whether there were differences by condition. The Chi square and Fischer's exact tests performed in Experiments 1&2 assume statistical interdependence, which is violated in a within subject, repeated measures design like what we used in Experiment #3. Instead, we used a Bhapkar test of marginal homogeneity, which allows for violation of independence of factors although this test requires a square matrix. To select 5 hallways for this matrix, we employed the same logic that we used to choose hallways for the Fischer's exact tests in Experiments 1 and 2. Hallways 4, 5, 6, and 14 are light and goal locations, and 9 and 10 can both be considered for the kinesthetic response strategy, so we averaged them to be the 5th response. Therefore, our 5 × 5 matrix used the 5 conditions and Hallways 4, 5, 6, the average of hallways 9 and 10, and 14.

Hypotheses. We predicted that the addition of body-based cues would lead to better encoding of the training path and therefore greater utilization of a place strategy. We also anticipated no main effect of condition because participants would likely stick with one strategy over all blocks. Alternatively, if we found a main effect of condition, this would suggest that individual participant strategy was malleable depending on the position of the light and other factors. Navigation strategies hypotheses remained identical to the general study hypotheses.

5.2. Results

15 datasets were analyzed after applying the exclusionary criteria.

We again considered how accurately participants found the reward location during each test trial across all participants. 12 out of 75 (16%) responses were the hallway that corresponded with an accurate shortcut. This was overall numerically consistent with what we observed in Experiments 1&2. Interestingly, only 2/75 (2.67%) responses were hallway 10, which would be consistent with a kinesthetic response strategy. However, including hallway 9 as a kinesthetic response strategy response, this number increased to 18/75 (24%) of all responses.

We fitted the hallway choice data based on condition to a multinomial log-linear regression model. The odds ratios calculated are shown in Figure 7B and indicate visually that participants choices varied as a function of condition, although with a somewhat consistent tendency to choose the response option (hallways 9/10). See Table 3 for numerical probability values. We conducted a likelihood ratio test comparing the results our regression model for the hallways chosen by condition to an intercept-only null model using a repeated measures ANOVA. We found a significant improvement over the null model ($F(4,56) = 3.3$, $p < .02$), suggesting a significant effect of condition on hallway choice.

Additionally, we conducted a Bhapkar Marginal Homogeneity test (Bhapkar, 1966) on hallways of interest to determine if these hallways were chosen differently based on condition. The Bhapkar test revealed a significant effect of the condition assigned on hallway chosen, $\chi^2(4) = 9.9838$, $p < .05$ We reran the Bhapkar's test two more times using the responses of only one of

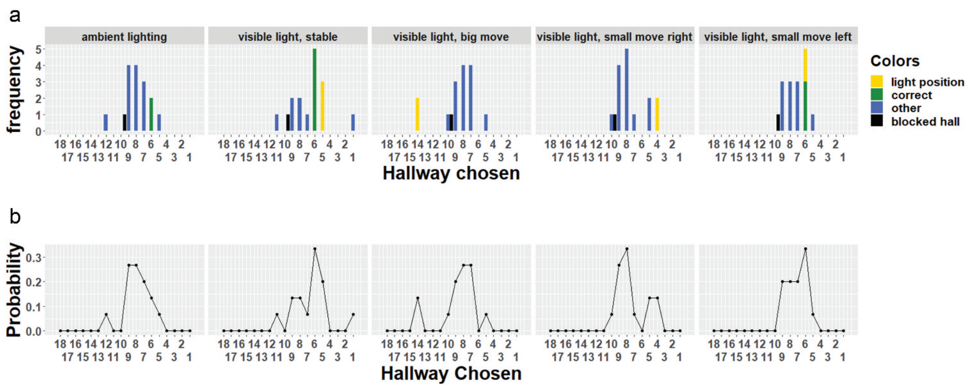

Figure 7. Experiment 3 frequency histograms of hallways chosen by condition (top row) and probabilities determined by multinomial regression (bottom row). (A) Frequency histograms that show the number of participants who chose each hallway separated by condition. (B) The probability that the participant will choose a given hallway when the condition assigned is known based on the multinomial regression. Reference condition is visible light, stable and reference hallway is 6.

Table 3. Experiment 3-fitted coefficients (p values) from multinomial log linear regression.

Hallway	Visible light, stable – intercept	Ambient Lighting	Visible light, big move	Visible light, small move right	Visible light, small move left
1	−1.609*	−16.788***	−6.768***	−7.040***	−24.422°
4	−15.814*	−4.703*	−1.615°	37.232*	−8.837***
5	−0.511*	−0.183*	20.635*	21.929*	−1.099*
7	−1.610*	2.015*	23.121*	22.335*	1.0998
8	−0.916*	1.609*	22.427*	23.250*	0.405*
9	−0.916*	1.609*	22.139*	23.027*	0.405*
10	−16.217*	−8.026***	36.342*	36.942*	−13.249***
11	−1.609*	−16.788***	−6.768***	−7.040***	−24.422***
12	−20.201***	19.508***	−0.895***	−0.879***	−8.936***
14	−16.484*	−4.836***	37.302***	−1.552***	−9.101***

Note: Hallways not displayed were not selected by participants in this experiment. Reference condition is visible light, stable and reference hallway is 6 (the 'correct' response). AIC value for this model = 346.287. NA was indicated as a p value when the values that were not able to be calculated, due to the hallway not being chosen by participants in this experiment. * p > 0.05, ** 0.05 > p > 0.005, *** p < 0.005, °NA.

these hallways (9 or 10) rather than averaging them. These results were also significant. Using only Hallway 9, Bhapkar's $\chi^2(4) = 14.492$, $p < .01$ and using hallway 10, Bhapkar's $\chi^2(4) = 14.849$, $p < .01$, we again found a significant dissociation across conditions. These findings suggested that, despite the presence of heightened body-based cues and a within-subject design, condition continued to influence participant hallway choice.

5.3. Discussion

Participant accuracy in Experiment 3 was comparable to the accuracy of the participants of Experiment 1&2 in terms of choosing the rewarded location from training during test (Hallway 6). This suggests that the presence of greater body-based cues and repeating the same locations during training, surprisingly, did not improve participant tendency to try to use a short-cut to the reward location. Instead, our results suggested that that participant memory for the rewarded location was influenced by the position of the light, despite what was likely stronger encoding from walking the paths and significantly more repetitions of the same rewarded location. In addition, these findings provide perhaps the clearest evidence for variable strategies, even in the same subjects, despite the reward location remaining constant.

6. General study discussion

Across three different experiments using the Tolman maze environment, we reported the same basic result: after encoding the location of a goal and provided with 18 different options to get there during test, participants most consistently employed a kinesthetic response strategy to get to the goal location. Surprisingly, despite hallway 6 providing the most direct pathway to the goal location, only a minority of participants selected this option (less than 20% in each of our different experiments). Instead, in the absence of any light cues, the majority of participants employed a kinesthetic response strategy. Our experiments further suggested that the light position acted as a significant cue that participants employed, in some cases, erroneously, to remember the location of the goal. In this way, our experiments provided the clearest evidence for both beacon responses (attempting to remember the position of the goal based on the position of the light) and kinesthetic responses (navigating the closest path to that of encoding). We found some (although limited) evidence for hybrid strategies, which in this case, would correspond to searching hallways somewhere in between the correct hallway (6), the kinesthetic response hallway (hallways 9/10), and the location that the light was moved to. Finally, we found some evidence for some participants using a place strategy, although these were a minority of subjects.

Experiment 1, which included a large sample of participants recruited through an on-line study, showed a clear effect of the position of the light on participant's choices for the goal location. In the ambient condition in which there was no light (identical to that used by Wilson & Wilson (2018), we found that the majority of participants employed a kinesthetic response, selecting hallway 9 or 10, similar to the results reported by Wilson and Wilson. When the light moved a large distance (from hallway 6 to hallway 14), like Wilson and Wilson, we found that a significant number of participants chose the hallway with the light location *during test*, significantly deviated from its position during encoding (at Hallway 5). Small movements of the light location from training to test also induced changes in where participants searched for the goal location, with both moves to the right and left significantly influencing participant choices of the goal location during test. These findings suggest that participants strategies are somewhat flexible and depend on combining different cues and memories. In this case, this would include their memory for the hallway they originally took and the light, which were both present during encoding, although neither was a “reliable” cue for the location of the goal (except when the light moved one hallway to the left, which corresponded with the actual location of the goal).

Previous studies have shown that extra-maze cues (such as distal landmarks) exert a significant influence over participant tendencies to take short cuts (Foo et al., 2005). To address this issue, in Experiment #2, we included prominent boundaries, whose corners and walls of different colors that could serve as distal cues (although depending on how participants used the cues, the boundaries could either serve as a beacon cue or allocentric cues). Despite the presence of these prominent cues, participants employed a place strategy at about the same rate (less than 20%) as they did in their absence in Experiment 1. The majority of participants again executed a kinesthetic response strategy when there were no light cues at encoding or test, yet switched their strategy based on the movement of the light. Like in Experiment 1, both larger and smaller movements of the light position influenced participant choices in the maze, suggesting that participants employed both beaconing and kinesthetic responses based on the cues present.

One potential limitation with the Wilson & Wilson study is that, unlike rodent studies, idiothetic cues were virtually absent as their studies (and our Experiments 1&2) were conducted in desktop VR. To attempt to address this issue, we tested participants on an omnidirectional treadmill. Surprisingly, despite the presence of both turning-related vestibular cues and other proprioceptive walking cues, participants showed no greater preference for the place strategy than Experiments 1&2. The majority of participants again appeared to favor the kinesthetic response strategy, also showing an influence of the light position on their memory for the goal location, suggesting a beacon response strategy. Because we employed a within-subject design here, this finding was perhaps most surprising: the same subjects encoded the same location repeatedly during encoding. Despite this, depending on the presence and location of the light, they chose different hallway locations. This suggests that, even in the same subjects, participants memories for the goal locations are influenced by familiar cues like lights and the path that they took previously.

One implication of our findings is that participant strategies during navigation are flexible. In other words, given available cues, participants utilize this information as an aid to remember the location of the goal, even when this information may not be particularly accurate or reliable. This type of flexibility is somewhat different than what was noted by Tolman in reference to the idea of a cognitive map. Tolman argued that representing the position of the goal (i.e., its direction and distance) relative to the extra-maze cues allowed for a flexible form of inference during testing. Our data would argue for a different form of flexibility: in the face of uncertain or noisy representations, participants may employ multiple strategies to try to remember where the goal was located. This is perhaps most evident in Experiment 3, which involved the same participants in all five conditions. Despite getting feedback on each testing trial about the position of the goal, participants continued to be influenced by the movement of the light, suggesting that how they remembered varied depending on the available cues.

It is also possible that participants failed to correctly encode the location of the goal because their path integration computations (via idiothetic cues) were too weak. We attempted to address this issue in Experiment 3 by strengthening idiothetic cues. Despite stronger idiothetic cues, only a minority of trials involved a place strategy. Given that participants in Experiment 3 repeatedly navigated (35 times) to the goal location during encoding, this should have provided sufficient repetitions to path integrate to the goal. As was suggested by Young et al. (1967), blind rats navigated correctly in the Tolman maze but when vision and extra-maze cues were added, these appeared to change the pattern of responses. Thus, the cues appear to provide a bias during training as to where participants remember the goal location.

It is also possible that participants perhaps encoded the environment accurately, but then chose a path that was not the shortest distance to the goal. For example, Muir and Taube (2004) tested rodents in the Tolman sunburst maze while simultaneously recording head direction cells in the anterior dorsal thalamus and post-subiculum. They found that while rodents often showed strong tuning in terms of head direction firing during training, this did not correlate nor predict their behavioral choices during test, which often involved many errors. This suggested that, at least in terms of neural activity, information may be encoded during training that is difficult to access subsequently during test. It is possible if we had told participants that they would need to remember the goal prior to training, this would have better promoted "carryover" from training to test. In this way, our study suggests that the incorporation of cues into spatial memory for the goal location may be reflective of spontaneous use of short cuts rather than deliberative ones. Notably, however, the conditions we tested are similar to those tested with rats, who cannot be explicitly instructed. In addition, the spontaneous use of short cuts is certainly one form of navigation that we are often faced with, for example, such as when we navigate a new city and are presented with an alleyway that could provide a more direct route. Our results suggest that under situations of new spatial learning in particular, we may employ cues and previous paths in place of somewhat unreliable memories for the goal location, leading to erroneous and non-optimal paths to the goal.

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Data availability statement

Figure data will be made publicly available on our website upon publication. http://humanspatialcognitionlab.org/open-source-data-supplemental-materials/

Disclosure statement

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ORCID

Stephanie Doner http://orcid.org/0000-0002-0338-5052

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