Probing the Invariant Structure of Spatial Knowledge:

Support for the cognitive graph hypothesis

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RUNNING HEAD: Probing the invariant structure of spatial knowledge

Abstract

We tested four hypotheses about the structure of spatial knowledge used for navigation: (1) the Euclidean hypothesis, a geometrically consistent map; (2) the Neighborhood hypothesis, adjacency relations between spatial regions, based on visible boundaries; (3) the Cognitive Graph hypothesis, a network of paths between places, labeled with approximate local distances and angles; and (4) the Constancy hypothesis, whatever geometric properties are invariant during learning. In two experiments, different groups of participants learned three virtual hedge mazes, which varied specific geometric properties (Control Maze, Elastic Maze, Swap Maze). Spatial knowledge was then tested using three navigation tasks (metric shortcuts, neighborhood shortcuts, route task). They yielded the following results: (a) Metric shortcuts were insensitive to detectable shifts in target location, inconsistent with the Euclidean hypothesis. (b) Neighborhood shortcuts were constrained by path boundaries in the Elastic Maze, but not in the Swap Maze, contrary to the Neighborhood and Constancy hypotheses. (c) The route task indicated that a graph of the maze was acquired in all environments, including knowledge of local path lengths. We conclude that primary spatial knowledge is consistent with the Cognitive Graph hypothesis. Neighborhoods are derived from the graph, and local distance and angle information is not embedded in a geometrically consistent map.

Keywords: human navigation, cognitive map, cognitive graph, spatial cognition

1. Introduction

As they explore the world, humans and other animals acquire knowledge of the spatial relations among features of their environment that guide navigation, such as the relative locations of landmarks and familiar places. Although the geometry of such spatial knowledge might take a variety of forms (Tobler, 1976; Trullier, Wiener, Berthoz, & Meyer, 1997; Tversky, 1993), a prominent view is that we build a metric *Euclidean cognitive map* (Figure 1A) of the environment (Gallistel, 1990; O'Keefe & Nadel, 1978; Piaget & Inhelder, 1956; Siegel & White, 1975; Tolman, 1948). At the other end of the spectrum, it has been proposed that spatial knowledge has a weak topological structure such as a *graph*. For example, a place graph captures only the network of paths connecting familiar places in the environment, with no metric information (Figure 1B, excluding labels) (Byrne, 1979; Kuipers, Tecuci, & Stankiewicz, 2003; Werner, Krieg-Brückner, & Herrmann, 2000). Another kind of topological structure is relations between *neighborhoods*, spatial regions bounded by paths or other environmental borders (Figure 1C). The location of a place may be described qualitatively by the neighborhood that contains it (Chase, 1983; Wiener & Mallot, 2003).

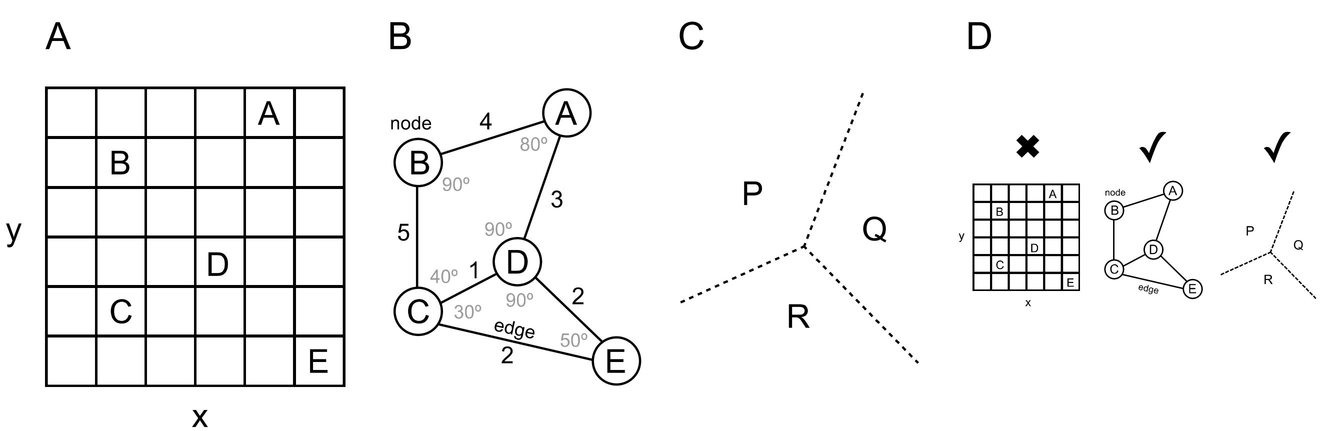

Figure 1. Models of spatial knowledge. (A) Euclidean map: places A, B, C… are assigned locations in a metric coordinate frame. (B) Labeled graph. In a topological graph, nodes correspond to places and edges to the paths connecting places. In a labeled graph, edge weights correspond to approximate distances between places, and node labels correspond to approximate

angles between paths; edge weights and node labels in a labeled graph need not be geometrically consistent. (C) Topological neighborhoods: Adjacency relations between spatial regions P, Q, and R, bounded by paths. (D) Another possibility is that spatial knowledge opportunistically preserves whatever geometric properties remain constant during learning.

An intermediate possibility that lies between Euclidean and topological structure is a *labeled graph*, such as a place graph augmented by approximate, local distance and angle information (Figure 1B, including labels) (Chrastil & Warren, 2014; Meilinger, 2008; Warren, Rothman, Schnapp, & Ericson, 2017). This structure has been called a *cognitive graph.* Others have proposed flexible or hybrid models combining the best features of Euclidean and topological models (Chown, Kaplan, & Kortenkamp, 1995; Kuipers, 2000; Mallot & Basten, 2009; Poucet, 1993; Truillier, Wiener, Berthoz, & Meyer, 1997).

To disentangle these models, experimenters have recently manipulated geometric properties of the environment using virtual reality displays (Warren, et al., 2017; Kluss, Marsh, Zetzsche, & Schill, 2015; Strickrodt, Meilinger, Bülthoff & Warren, 2020). However, this approach raises the possibility that spatial knowledge reflects whatever geometric properties remain invariant during learning—a constancy hypothesis that to our knowledge has not been previously tested.

In the present study, we sought to systematically evaluate four hypotheses about the geometry of spatial knowledge: (1) the Euclidean hypothesis, which posits that primary spatial knowledge has the properties of a metric Euclidean map; (2) the Cognitive Graph hypothesis, that primary spatial knowledge is characterized by a labeled (cognitive) graph; (3) the Neighborhood hypothesis, that primary spatial knowledge consists of adjacency relations between spatial regions; and (4) the Constancy hypothesis, that spatial knowledge preserves the specific geometric properties that remain invariant during learning. Taken together, these four hypotheses span the spectrum of proposed forms of spatial knowledge. By testing them in a single study, we aim to zero in on the geometric properties that constitute primary spatial knowledge, from which weaker properties might be derived. We now elaborate each hypothesis in turn.

1.1 Euclidean hypothesis

The term “cognitive map” was introduced into the field by Tolman (1948), who reported that rats often take direct (i.e., “as the crow flies”) novel shortcuts to a trained location. Similar behavior was subsequently reported in a variety of animals (Chapuis, Durup, & Thinus-Blanc, 1987; Chapuis, Thinus-Blanc, & Poucet, 1983; Menzel, 1973; Gould, 1986; Wehner, Michel, & Antonsen, 1996), reinforcing the concept of a cognitive “survey map” with a metric Euclidean structure (O’Keefe & Nadel, 1978; Piaget & Inhelder, 1956; Siegel & White, 1975). Such a map could be constructed by means of path integration, based on idiothetic (proprioceptive, motor, and vestibular) information about distances traveled and angles turned while learning an environment, by embedding these local measurements into a geometrically consistent coordinate system (Gallistel, 1990; Bush, Barry, Manson & Burgess, 2015; McNaughton, Battaglia, Jensen, Moser & Moser, 2005; Moser, Moser & McNaughton, 2017). A Euclidean map would be advantageous because it captures all geometric relations among learned locations including distances and directions, and thus enables novel routes and shortcuts using trigonometry (Gallistel, 1990).

On the other hand, alternative explanations have been offered for claims of novel shortcuts in animals, including beacon homing (Dyer, 1991), familiar routes (Bennett, 1996; Collett & Collett, 2006), and “snapshot matching” (Cartwright & Collett, 1983; Wehner, et al., 1996) (see Warren, 2019, for a review). In humans, directional estimates are highly inaccurate and imprecise, with absolute directional errors ranging from 20˚- 100˚, and standard deviations reaching 30˚ (Chrastil & Warren, 2013; Foo et al., 2005; Ishikawa & Montello, 2006; Meilinger, Riecke, & Bülthoff, 2014; Schinazi et al., 2013; Waller & Greenauer, 2007). Most humans cannot successfully integrate separately-learned routes, even after repeated exposure (Ishikawa & Montello, 2006; Weisberg, Schinazi, Newcombe, Shipley, & Epstein, 2014). Many studies of human spatial cognition imply violations of the metric postulates, which must be satisfied by a Euclidean map (see Warren, et al., 2017, for a review).

Collectively, this research provides little evidence for the Euclidean hypothesis that humans and other animals acquire a geometrically consistent metric map. Nevertheless, opinion remains divided and the Euclidean view retains many supporters (Byrne, Becker, & Burgess, 2007; Cheeseman et al., 2014; Jacobs & Schenk, 2003; Moser, Moser, & McNaughton, 2017; Nadel, 2013).

1.2 Cognitive Graph hypothesis

A topological place graph captures a network of paths linking places in the environment. Nodes in the graph correspond to familiar places, and edges correspond to familiar paths between them (Mallot and Basten, 2009; Poucet, 1993). A place graph preserves the connectivity among places and their ordinal relations, but no information about distances and angles. They thus enable novel routes and detours, but do not support novel shortcuts. One advantage of a topological graph is that it is more robust and less vulnerable to noise and error than a Euclidean map, because the topology of the environment is preserved even when metric properties are not accurately acquired.

A labeled graph augments a purely topological graph with rough, local information about distances and angles (Figure 1B; Warren et al., 2017). Nodes corresponding to salient places are labeled with approximate junction angles between paths, while edge weights express approximate path lengths between places. The path integration system is suited for registering such rough, piecewise path lengths and turn angles, given its poor resolution, systematic biases, and error accumulation (Warren, 2019). What distinguishes a labeled graph from a metric map is that this local information is not embedded into a geometrically consistent coordinate system (a 'global metric embedding'). Spatial knowledge may thus be geometrically inconsistent and violate the metric postulates. Nevertheless, such a cognitive graph would support approximate novel shortcuts by vector addition through the graph, often sufficient to bring the navigator within sight of a beacon near the goal (Warren, et al., 2017).

Previous studies have investigated several predictions that follow from the Cognitive Graph hypothesis. For example, Chrastil and Warren (2014, 2015) asked participants to take routes between learned places in a virtual hedge maze, and found that the metrically shortest paths were preferred when taking both direct routes and novel detours. This result implies more than topological knowledge is acquired, consistent with a labeled graph.

Warren et al. (2017) investigated the spatial knowledge acquired in a non-Euclidean virtual environment. Participants learned a geometrically impossible virtual hedge maze containing two 'wormholes,' which covertly teleported them 6m or 10m and rotated them by 90˚ visually. The Euclidean hypothesis predicts that the non-Euclidean maze should be more difficult to learn, but because participants are trained to the metric locations of target objects, shortcuts should be similar in the Wormhole maze and a matched Euclidean maze. In contrast, if a labeled graph of the environment is acquired, the course of learning should be similar in both mazes, and shortcuts should be biased by the wormholes. Consistent with the Cognitive Graph hypothesis, the mazes were equally difficult to learn, shortcuts were strongly biased by the wormholes, and participants were completely unaware of any geometric discrepancies. Path integration thus failed to reveal the geometric inconsistency of the Wormhole maze. The same results were obtained when visible distal landmarks were added, indicating that allocentric information likewise failed to reveal the inconsistency (Ericson & Warren, in preparation). Because shortcuts were directional rather than uniformly distributed on the circle, however, the results were also inconsistent with a purely topological graph.

Subsequently, Strickrodt, Meilinger, Bülthoff, and Warren (2020) asked participants to learn the locations of objects in another impossible maze, a loop of zig-zagging corridors that was completed by a covert teleportation. They found that the magnitude of pointing error to each object was predicted by the local distances and angles participants had walked during learning. These findings indicate that the spatial knowledge preserves local metric information, but does not embed it in a geometrically consistent coordinate system, supporting the Cognitive Graph hypothesis.

1.3 Neighborhood hypothesis

A complementary form of topological structure can be described in terms of neighborhoods. A neighborhood is a region whose boundaries are defined by a 'skeleton' of major paths or other salient environmental borders such as a river or forest edge (Figure 1C) (Kuipers, Tecuci, & Stankiewicz, 2003; Wiener & Mallot, 2003). Topological relations between neighborhoods include adjacency (regions sharing a common border) and inclusion (one region contained within another) (Randell, Cui & Cohn, 1992), and places can be localized by the neighborhood that contains them (Chase, 1983). Conversely, to the extent that neighborhood boundaries are defined by paths between places, neighborhoods may be derived from a place graph[1] (Kuipers, et al., 2003), such as the regions bounded by edges to nodes in Figure 1B.

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[1] Note that one may construct a complementary neighborhood graph, in which nodes correspond to neighborhoods and edges to adjacency relations.

Alternatively, metric neighborhoods can be derived from Euclidean relations between the locations of places and the locations of environmental boundaries.

Several studies suggest that humans use topological strategies when navigating to the remembered locations of targets, including the ordinal structure of places (Zhong et al., 2005, 2007) and the neighborhoods defined by major paths (Chase, 1983; Pailhous, 1969; Weiner & Mallot, 2003; Wiener, Schnee, & Mallot, 2004; Zhong, et al., 2006). Research on the neurophysiological basis for navigation suggests that the hippocampus may be involved in building a topological graph (Dabaghian, Mémoli, Frank, & Carlsson, 2012; Muller, Stead, & Pach, 1996), and topological strategies have also proven successful in the context of robot navigation (Thrun & Bücken, 1996).

1.4 Constancy hypothesis

Shortcuts and pointing to learned locations exhibit large variable errors that are similar in impossible virtual environments, matched Euclidean environments, and real environments (Section 1.1), implying a comparable imprecision in spatial knowledge. Nevertheless, it is logically possible that participants in an impossible maze learned a labeled graph, whereas those in a Euclidean maze and the real world learned a metric map, consistent with a hybrid model (e.g. Mallot & Basten, 2009; Poucet, 1993; Truillier, et al., 1997). In other words, spatial knowledge may opportunistically reflect whatever geometric properties remain invariant during learning, which we refer to as the Constancy hypothesis.

1.5 The present study

The present experiments aimed to test these four hypotheses about spatial knowledge (Euclidean, Neighborhood, Graph, Constancy hypotheses) by selectively varying the geometric properties of the environment during learning (metric, neighborhood, and graph structure). This was accomplished by manipulating three virtual hedge mazes, as follows. (i) The Control Maze was a Euclidean environment that preserved all geometric properties. (ii) In the Elastic Maze, certain corridors alternately stretched from a short to a long length, so that the same object occupied two metric locations (short and long) in different neighborhoods or on different paths. This varied the Euclidean structure and the metric neighborhood containing the object, while preserving the original place graph. (iii) In the Swap Maze, pairs of objects alternated between two locations within the same neighborhood; this varied the nodes and edges in the graph that led to the 'place' defined by an object, while holding constant the neighborhood that contained that object.

In the test phase we probed the resulting spatial knowledge using three corresponding navigation tasks: (a) the *metric shortcut task* asked participants to take direct shortcuts from a *start* object to a *target* object, with only the ground plane visible; (b) the *neighborhood shortcut task* modified this by adding visible neighborhood boundaries (outlines of the three major paths) on the ground during shortcuts; and (c) the *route task* asked participants to walk in the maze to the path containing the target, and then down a visually infinite corridor to the remembered position of that target. Each task in each maze was performed by a different group of participants.

This design yielded the following predictions for each hypothesis. (1) The Euclidean hypothesis posits that primary spatial knowledge corresponds to a metric Euclidean map. When building a map, given that normal path integration is somewhat noisy, the varying measurements would be embedded in the map at coordinates corresponding to the average location, with some uncertainty. In the Elastic Maze, the metric location of the elastic target varies, so the hypothesis predicts that metric shortcuts should be close to the average position of the short and long targets, and be more variable than in the Control Maze. Second, if neighborhoods are derived from Euclidean relations, then participants should be able to detect when a target is in the short or long neighborhood, even when the boundary is not visible, based on path integration. Consequently, neighborhood shortcuts (and possibly metric shortcuts) should be more variable and more bimodal in the Elastic Maze than the Control Maze. Finally, if a labeled graph is derived from Euclidean knowledge, path choice in the route task should be bimodal in the Elastic Maze, because the target is stretched to coordinates that fall on a different path. The target's estimated position along the stretched path should be similar to metric shortcuts to the same coordinates.

(2) The Neighborhood hypothesis proposes that the primary structure of spatial knowledge consists of adjacency relations between topological neighborhoods bounded by visible paths (the 'skeleton'). Zhong et al. (2006) found that when paths were visible during learning and testing, shortcuts were more precise, implying that neighborhoods are acquired. In the Elastic Maze, a target is stretched to coordinates that lie in a different neighborhood, so metric neighborhoods vary; however, the participant does not cross a visible boundary (an intersection) when walking down a stretched path, so the target remains in the same topological neighborhood. Thus, the Neighborhood hypothesis predicts that neighborhood shortcuts should be unimodal, and comparable to those in the Control Maze. In the Swap Maze, targets switch locations within in the same neighborhood, so the hypothesis also predicts that neighborhood shortcuts should be unimodal and comparable to the Control Maze.

(3) The Cognitive Graph hypothesis posits that the primary structure of spatial knowledge corresponds to a labeled place graph, with approximate path length and angle information. In the Elastic Maze, when metric structure is varied, the hypothesis predicts that the chosen path to a

target should be correct and unimodal, similar to the Control Maze. However, because the graph is labeled with rough path lengths, the estimated target position along the path should be close to the average location, and be more variable than in the Control Maze. In contrast, in the Swap Maze, when edges in the graph leading to the same 'place' alternate, the hypothesis predicts that path choice to a target should be bimodal.

(4) Finally, the Constancy hypothesis posits that spatial knowledge reflects the specific geometric properties that remain invariant during learning. If this hypothesis is correct, performance should always be consistent with whatever environmental properties are held constant as other properties are varied. Specifically, in the Control Maze, when metric structure is invariant, shortcut performance should reflect Euclidean knowledge. In the Elastic Maze, when the place graph is invariant while metric structure is varied, performance should reflect graph knowledge. In the Swap Maze, when the place graph is varied while neighborhoods (defined by visible boundaries) are constant, performance should reflect neighborhood knowledge.

We found that the spatial knowledge acquired in these environments was neither Euclidean nor purely topological, nor did it reflect the geometric properties that were invariant during learning. The results support the Cognitive Graph hypothesis.

2. Experiment 1: The Elastic Maze (invariant graph)

Experiment 1 investigated the Euclidean, Neighborhood, and Graph hypotheses by comparing the Elastic Maze to the Control Maze. The Elastic Maze was designed to vary Euclidean structure (and hence metric neighborhoods) during learning, while holding the place graph (and hence topological neighborhoods) constant. In contrast, the Control Maze held Euclidean structure constant, and so all geometric properties remained invariant during learning.

The experiment consisted of three phases: *free exploration*, in which the participant explored the maze to learn object locations; the *training phase*, in which the participant was trained to find each object from a central home location until they reached criterion; and the *test phase*, in which participants performed a navigation task without feedback. (We refer to first two jointly as the *learning phase*.) The three navigation tasks assessed acquired knowledge of the corresponding properties: metric shortcuts assessed Euclidean knowledge, neighborhood shortcuts assessed knowledge of metric and topological neighborhoods, and the route task assessed graph knowledge. This design resulted in six conditions (2 Environments x 3 Tasks), with a separate group of 12 participants in each condition.

2.1 Predictions

The hypotheses described in Section 1.5 yield specific predictions for each navigation task, which we state here (refer to Table 1).

2.1.1 Metric shortcut task

Prediction 1: If primary spatial knowledge is Euclidean, then metric shortcuts in the Elastic Maze should shift to the average of the short and long target locations, and be more variable, compared to the Control Maze. This should also be the case for probe trials compared to control trials in the Elastic Maze. *Prediction 2*: Alternatively, if primary spatial knowledge resembles a rough labeled graph, we might expect that metric shortcuts are directional but similarly unreliable in both mazes, and on both types of trials; although this could also result from Euclidean spatial knowledge that is highly imprecise.

2.1.2 Neighborhood shortcut task

Prediction 3: If metric neighborhoods are derived from Euclidean knowledge, then shifting the target between the short and long neighborhoods in the Elastic Maze should yield neighborhood shortcuts that are bimodal and more variable than in the Control Maze, and on probe trials than control trials. *Prediction 4:* Under the Neighborhood hypothesis, topological neighborhoods are defined by visible boundaries, yet no visible path intersections were crossed in the stretched hallways. The hypothesis thus predicts that neighborhood shortcuts in the Elastic Maze should be unimodal (in the short neighborhood) and similar to those in the Control Maze, and probe trials should also be similar to control trials. In addition, they should be less variable than the corresponding metric shortcuts.

2.1.3 Route task

Although the Elastic Maze varied metric structure, the topological graph of the environment was preserved. The route task was designed to probe graph knowledge, leading to the following predictions. *Prediction 5*: If graph knowledge is derived from Euclidean structure (i.e., from metric relations among places and paths), (5a) path choice should be bimodal in the Elastic Maze because the coordinates of short and long targets fall on different paths, and (5b) estimated target positions along the stretched paths should be similar to metric shortcuts to the same targets. *Prediction 6*: If primary spatial knowledge resembles a labeled graph, then (6a) path choice should be unimodal and correct (to the 'short' target location) in the Elastic Maze despite varying metric structure, and (6b) estimated target position along the stretched path in the Elastic Maze should shift to the average target location compared to the Control Maze, and be less variable than metric shortcuts.

2.2 Method

2.2.1 Participants

A total of 91 people participated in the experiment; of these, 72 (36M, 36F) completed the study and were included in the analysis. Eight participants withdrew due to symptoms of simulator sickness. Two participants in the Control Maze were excluded for failing to reach criterion during the training phase. Nine participants were excluded due to technical problems in the first session. This resulted in six groups, each consisting of 12 participants (6M, 6F). Participants were recruited through advertisements and were paid for their participation. All participants provided informed consent in accordance with the requirements of Brown University's Institutional Review Board.

2.2.2 Apparatus

Participants walked freely within a 10.5m x 12.5m tracking area during the experiment; if they walked outside this area, virtual brick walls appeared approximately 1m in front of them to prevent collisions with the physical walls. Stereo images of the virtual environment were generated on a graphics workstation (Dell XPS 730X, NVIDIA GTX 280 graphics) and presented in a head-mounted display (HMD, Rockwell-Collins SR80, 1280x1024 pixels, 63° H x 53° V field of view for each eye). The computed disparity and lens separation were calibrated to each participant's measured inter-ocular distance. An ultrasonic/inertial tracking system (InterSense IS-900, 50ms total latency, 1.5mm/0.10° spatial resolution) recorded the participant's head position, and they carried a wireless mouse with response buttons. Background noise (crickets) was played over wireless headphones, and the view of the lab was blocked by a dark cloth draped over the HMD.

2.2.3 Displays

The virtual environments were hedge mazes containing a central home location (home plate), three primary corridors in a 'Y' configuration, with ten distinctive objects (moon, bookcase, etc.; see Figure 2A) located at the ends of secondary (i.e. terminal) corridors. Four paintings also appeared on the walls in the main corridors to serve as orientation aids. Objects were not visible from the main corridors, so participants had to walk between them. The Control Maze had a constant Euclidean geometry similar to the real environment.

The Elastic Maze was identical except for four hallways that covertly changed length on each pass during the free exploration and training phases. Four *probe* objects at the ends of these elastic hallways alternately appeared in the canonical location (short position), matching the Control Maze, and stretched by 3m (long position) (see Figure 2B). For two of these probes (Moon and Gear), the stretched target shifted across a primary path into an adjacent neighborhood, and for three probes (Moon, Bookcase, Clock), the stretched target shifted into a different terminal corridor. As the participant walked down the stretched hallway, however, no intersections were visible. The alternation was triggered by invisible gates near the hallway entrance, which loaded the appropriate hallway before it came into sight. The initial view (canonical or stretched) was randomized across participants and probe objects. Alternations were visually seamless and all textural elements (wall, floor) in the maze were matched and updated in one frame (roughly 1/60s). Stretched targets were in principle detectable based on (1) the visually perceived distance to the probe target from the start of the hallway, or (2) the walked distance to the probe target from the start of the hallway, by path integration.

2.2.4 Design

Experiment 1 had a 2 x 3 x 2 design, with two environments in the learning phase (Elastic Maze, Control Maze) crossed with three navigation tasks (Metric Shortcut, Neighborhood Shortcut, Route) and two trial types (Probe, Control) in the test phase. Environment and task were between-subjects factors, and trial type was the within-subject factor. Each participant experienced only one virtual environment and one response task, and trial order was randomized for each participant.

2.2.5 Procedure

Each participant completed two sessions. The first session included the free exploration phase (12 minutes), training phase (< 25 min), and test phase (18 trials), and lasted approximately 1hr. The second session included refresher training (< 25 min), further testing (54 trials), and a debriefing, and lasted 1.5 - 1.75 hours. At the beginning of *free exploration,* participants were instructed to try and find all the objects in the maze and learn their locations, for they would be tested on their knowledge of the objects and their locations later. They then freely explored the maze for 12 min.

During the *training phase*, participants were trained to find each of the objects from home until they reached the criterion of finding each object in less than 30s two times. If a participant found an object in 30-45s, the object was repeated later. If the participant could not find an object after 45s, they returned home and the experimenter silently guided them by the shoulders along the most direct route to the object, and they were asked to find the object again later. If a participant failed to reach the training criterion within 25 min, testing was terminated and they were removed were removed from the experiment.

In the test phase, participants were instructed to perform one of the three navigation tasks to assess the spatial knowledge acquired during learning. Eight object pairs were tested: four

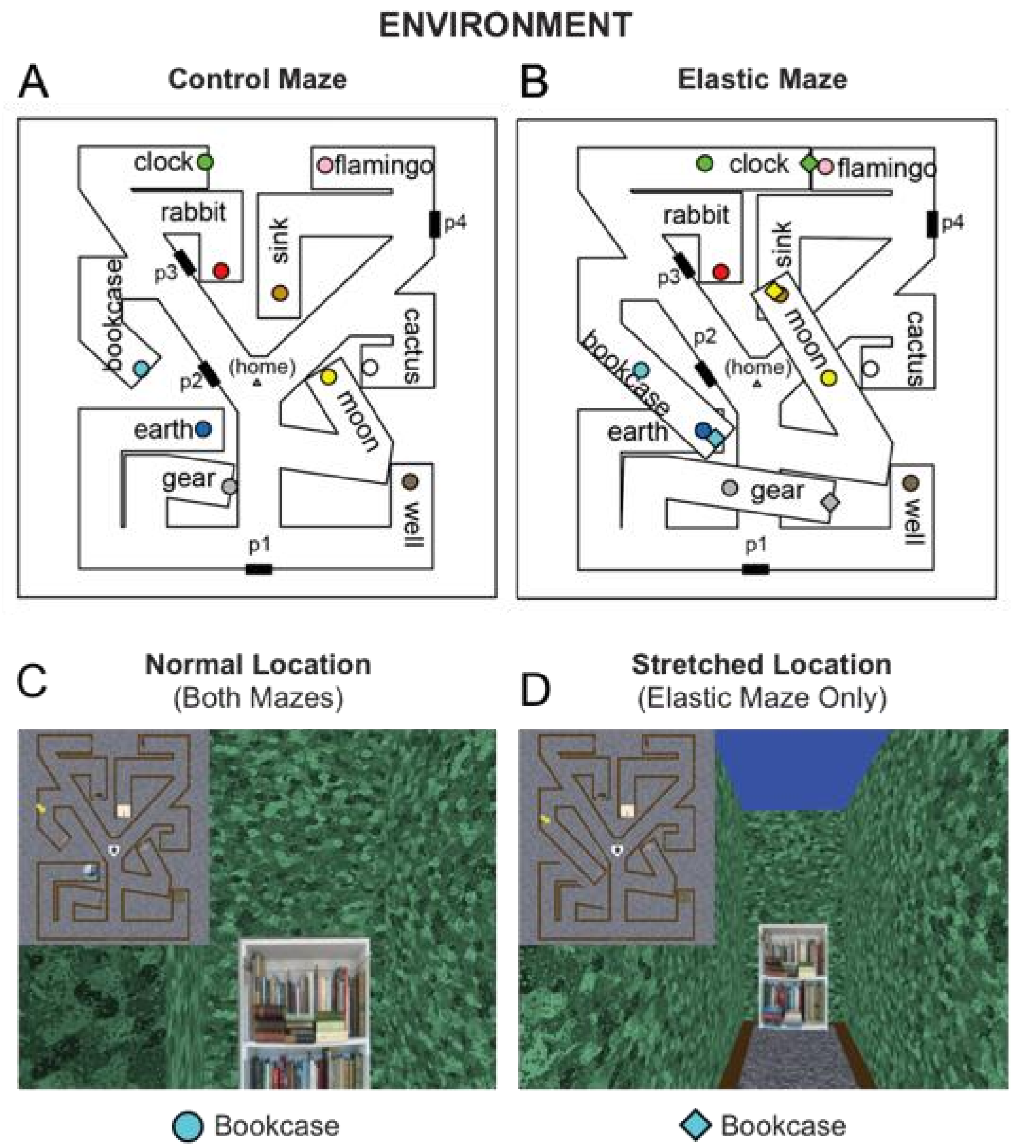

Figure 2. Experiment 1: mazes and displays. Both the Control Maze (A) and Elastic Maze (B) contained 10 distinctive objects, four paintings (p1-4) that served as local landmarks, and a central home location (home plate). Objects were designated control (well, sink, cactus, rabbit, flamingo, earth) objects if they remained in the same location in both environments, and probe (bookcase, clock, moon, gear) if their paths were alternately stretched in the Elastic Maze. In the Elastic Maze (B), two probe objects were stretched (D) across a neighborhood boundary (moon, gear), and three targets (moon, bookcase, clock) were shifted to coordinates in a different terminal corridor. Overhead views of each maze (shown in the top left corner of panels C and D) were not visible to participants.

control pairs (sink→earth, rabbit→well, earth→sink, well→flamingo) and four probe pairs (sink→bookcase, rabbit→gear, earth→moon, well→clock) (Figure 2). For each pair, the participant first walked to a *start* object in the maze corridors, and then to the remembered location of a *target* object (note that the same four objects served as start objects in probe and control trials, whereas the target objects differed). On probe trials the target was in an elastic hallway, whereas on control trials the target was in a normal hallway. Each participant made a total of 72 responses ((4 probe pairs + 4 control pairs) x 9 repetitions) during the test phase.

The metric shortcut task was designed to assess metric Euclidean knowledge. On each trial, the participant walked from home to the start object; at that point the maze walls, objects, and paths disappeared, leaving only a randomly textured ground plane (Figure 4A). The participant then faced the remembered location of the target object and clicked the mouse to indicate their alignment with the target. Finally, they walked in a straight line to the remembered location of the target, stopped and clicked the mouse again. Participants did not receive feedback, and were passively wheeled in a wheelchair back to home along a circuitous route for the next trial.

The neighborhood shortcut task was designed to assess neighborhood knowledge. The procedure was the same as the metric shortcut task, except that the outlines of the three primary paths (neighborhood boundaries) remained visible on the ground during shortcuts in the test phase (Figure 4B). Recall that no path intersections appeared in the stretched hallways during learning. Thus, if participants learned which topological neighborhood contains the target based on visible boundaries, shortcuts to probe targets in the Elastic Maze should be unimodal (within the short neighborhood), similar to the Control Maze and to control trials, and less variable than the metric shortcut task. On the other hand, if neighborhoods are derived from metric information about the locations of objects and hallways, shortcuts should be more variable than in the Control Maze, and those to the Moon and the Gear more bimodal.

In the Route Task, participants walked from Home to the start object, whereupon all objects disappeared, but the maze walls remained visible. Participants then walked within the maze corridors to the remembered location of the target. If they entered a terminal hallway that had contained an object, it was displayed as a visually infinite (~300m) corridor with no intersections (Figure 4C); this was done for all terminal hallways on both control and probe trials to prevent feedback about the correct path. They then walked down the infinite corridor to the remembered location of the target, stopped and clicked the mouse. If participants learn a place graph of the maze, path selection should be highly accurate. If they also acquire local information about distance or path length (i.e., edge weights), the responses should be biased toward the average target position in the elastic hallways. Recall, however, that the 'short' and 'long' coordinates of the Moon, Bookcase, and Clock fell in different terminal corridors. So if participants derive a graph from Euclidean locations, one would expect a bimodal pattern of path choice on these probe targets.

In a *debriefing,* participants were given a list of objects and asked to create a hand-drawn map of the maze, and answered a series of questions about their experience in the virtual environment and prior experience playing video games. Then then completed three spatial abilities tests, to assess any differences in spatial abilities between groups: (1) the Santa Barbara Sense of Direction Scale (SBSOD; Hegarty, Richardson, Montello, Lovelace & Subbiah, 2002), (2) a Road Map Test (RMT; Money & Alexander, 1966; Zacks, Mires, Tversky, & Hazeltine, 2000); and (3) the Perspective-Taking and Spatial Orientation Test (PTSOT; Kozhevnikov & Hegarty, 2001; Hegarty & Waller, 2004). The SBSOD asks for self-ratings of spatial abilities along a number of dimensions. The RMT assesses perspective-taking ability by having participants name the sequence of left and right turns they would need to make to follow a route plotted on a road map. The PTSOT assesses perspective-taking ability by having participants estimate directional relationships among iconic representations of objects arranged on a page. Finally, they were asked to verbally report anything they noticed about the virtual environment.

2.2.6 Data analysis

We analyzed the positional data (x, y, t) from the Intersense IS-900 head-tracking system. Data were analyzed using Python, R (version 2.15.2; "Circular" package, Agostinelli & Lund, 2013; "Circstats" package, Lund & Agostinelli, 2007), MATLAB (MathWorks), Oriana (Kovach Computing Services) and SPSS (IBM).

To quantify the extent and homogeneity of free exploration, invisible "gates" were placed throughout the maze that recorded when a participant passed that location. Several measures were extracted from the training phase to assess the learning process, including the total number of trials needed to reach criterion, and the number of trials in which a participant needed to be guided to the objects.

For test trials, dependent measures were extracted from walking trajectories between the button press at the start object and that at the target. Shortcut trajectories that intersected with the emergency walls during the test phase (Control Maze: metric shortcuts, 35%; neighborhood shortcuts, 15.3%; route task, 0%; Elastic Maze: metric shortcuts, 43.8%; neighborhood shortcuts, 18.7%; route task, 0%) were excluded from the calculation of 95% confidence ellipses.

The primary dependent measures were based on directional (angular) errors. Although the (unsigned) absolute error (AE) is a common measure in the navigation literature, it confounds the (signed) constant error (CE), a measure of accuracy, and the variable error (VE), a measure of precision. Angular CEs were computed with respect to the "canonical" locations of targets in the Control Maze. Specifically, constant error was the signed angle (-180º, +180º] between two vectors defined by (1) the participant's starting location and the endpoint of their response, and (2) the participant's starting location and the canonical target location. CEs on probe trials were normalized so that 0º corresponded to walking toward the canonical target location and positive values corresponded to walking in the direction of the stretched target location. The von Mises distribution—a circular analogue of the normal distribution—was used to model directional responses, and the Watson-Williams test—a circular analogue of ANOVA—was used to compare angular CEs. Because two-way Watson-Williams tests are not currently available, main effects for CEs were examined using one-way Watson-Williams tests, and the results of pairwise, post-hoc Watson-Williams tests are shown as Duncan groupings in graphs.

Variable error was measured by the between-subject angular deviation (AD), the circular equivalent of the standard deviation (SD). To estimate individual precision, we also computed the mean within-subject AD (mean within-subject SD for linear variables) for each participant. Circular means were computed for all angular variables. Absolute error and variable error were analyzed using ANOVA. Following Howell (2008), follow-up tests on repeated measures (mixed-model) ANOVAs were conducted using Tukey's HSD procedure, to maintain a family-wise error rate of $\alpha = .05$ for multiple comparisons.

To complement these frequentist statistics, we also took a Bayesian approach. First, Jeffrey-Zellner-Siow (JZS) Bayes Factors were computed from the ANOVA results to compare the strength of evidence for the Null (M_0) and Alternative (M_1) hypotheses (Faulkenberry, 2018). In addition, when two of our hypotheses could be modeled by the von Mises distribution (model M_i, with parameters $\theta_i = [\mu_i , \kappa]$) and predicted unique responses, we compared models by computing the JZS Bayes factor, $BF_{10} = p(\text{Data}|M_1)/p(\text{Data}|M_2)$, where $p(\text{Data}|M_i)$ is the likelihood of the data under M_i. The concentration parameter κ was estimated from the AD for the same task in the Control Maze and held constant (Batschelet, 1981). According to the revised scheme of Nuijten, Wetzels, Matzke, Dolan, & Wagenmakers (2015; based on Jeffreys, 1998), $BF_{10} < 1$ indicates no evidence for M_1; $1 < BF_{10} < 3$, anecdotal evidence for M_1; $3 < BF_{10} < 10$, substantial evidence for M_1; $10 < BF_{10} < 30$, strong evidence for M_1; $30 < BF_{10} < 100$, very strong evidence for M_1; and BF > 100, decisive evidence for M_1 (and the inverse for M_0). To avoid over-fitting and for purposes of clarity, only effects relevant to the predictions of the four hypotheses will be described.

Just noticeable differences (JNDs) were estimated to determine whether targets in the Elastic Maze were stretched far enough to be detectable by the participant during learning, given the observed variability in the Control Maze. Estimated JNDs were obtained for each task by multiplying the mean within-subject AD for each probe target in the Control Maze by 0.8099, corresponding to 75% of the area under the von Mises distribution (with κ=1). The *stretch angle* of each target in the Elastic Maze was the angle subtended by the short and long target locations, as measured from the start object (the vertex) (Earth → Moon, 40.3º; Sink → Bookcase, 23º; Well → Clock, 15.2º; Rabbit → Gear, 37.2º); the circular mean was 28.9º. If the JND is smaller than the stretch angle, then that target was stretched far enough to be detectable during learning.

Two approaches were taken to analyzing the bimodality of metric and neighborhood shortcuts. First, CEs for shortcuts to each of the probe targets were submitted to two-component cluster analyses using the k-means algorithm (Forgy, 1965; Hartigan & Wong, 1979; Lloyd, 1982). The k-means method attempts to divide a collection of data points into *k* groups ($k = 2$ assesses bimodality) using a least squares criterion. Following Hill & Lewicki (2005) we compared the magnitude of the resulting F-ratio in the Elastic and Control Maze. Second, constant errors were examined by fitting kernel density estimates for mixtures of von Mises distributions using the maximum likelihood cross-validation (MLCV) method, which is sensitive to bimodality in directional data (Agnostinelli & Lund, 2011; Sharma & Tarboton, 1997).

Endpoint analysis provided measures of how often shortcut endpoints fell in different neighborhoods (Figure 3A). For example, in the Elastic Maze, the Moon and the Gear were stretched from the canonical (short) neighborhood into an adjacent (long) neighborhood during learning. Classifying the number of endpoints falling in the short or the long neighborhood allows us to assess the neighborhood knowledge in each maze. Shortcuts that ended on a maze path or in a neighborhood that did not contain the target were classified as *path* and *wrong* respectively.

To determine whether participants learned the graph of the maze, path choices in the Route Task were classified as correct if they walked down the hallway that contained the target, and incorrect if they walked down any other terminal hallway (Figure 3B). *M* and *SD* of the number of correct and incorrect path choices were obtained for each target for each participant. To analyze the bimodality of path choices, we compared the number of paths (i) corresponding to short and long target locations in Experiment 1 (see Figure 3) and (ii) corresponding to canonical (A) and non-canonical (B) target locations in Experiment 2 (see Figure 7).

Finally, sketch maps were analyzed using Gardony's (2016) Map Drawing Analyzer Software, which provided measures of both relative and absolute landmark placement, and bidimensional regression analyses (Friedman & Kohler, 2003; Tobler, 1994) compared drawn configurations to the actual configuration of objects in the Control Maze.

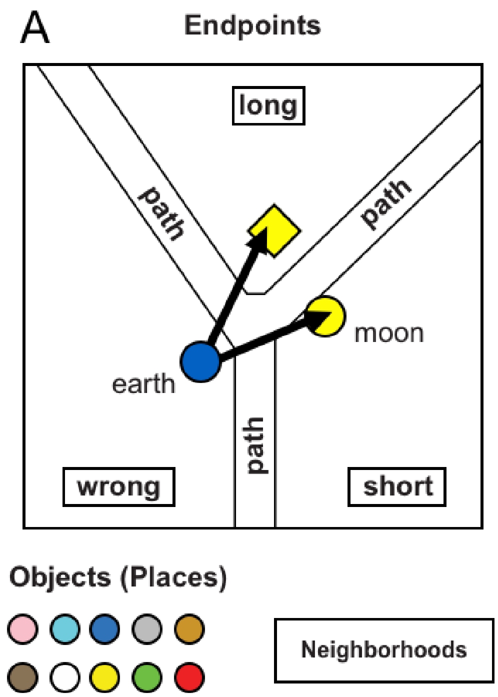

Figure 3. Experiment 1: classification scheme for endpoints and path choices. For example, in the Elastic Maze, the Moon alternately occupied short (*yellow circle*) or long (*yellow diamond*) neighborhood locations during learning. The following endpoint (A) and path choice (B) classification schemes were applied to shortcuts in both Mazes. (A) Percentages of endpoints falling in each of the four possible regions (long, short, wrong neighborhood, or path) were computed for each participant. (B) Paths were classified as correct if they walked down the target object's path, and incorrect if they walked down any other path.

2.3 Results

Sample traces of shortcuts (earth→moon) in the Control Maze and the Elastic Maze are plotted for each of the three tasks in Figure 4. For each object pair, a mean shortcut vector was computed based on the mean CE, and the mean distance from start points to endpoints.

2.3.1 Free exploration and training phases

Visual inspection of position traces confirmed that participants in the Elastic Maze physically walked to the stretched locations of probe objects during free exploration. An ANOVA on the mean number of visits to probe and control objects revealed a significant main effect of trial type, $F(1,66) = 19.42$, $p < .001$, $\eta_G^2 = .044$, and a Bayesian equivalent indicated anecdotal evidence for the alternative hypothesis (BF_{10} = 2.858). A post-hoc Tukey test revealed that participants visited probe objects (*M* = 4, *SD* = 0.89) more frequently than control objects (*M* = 3.66, *SD* = 0.08), $p < .05$. No other significant effects, interactions, or between-subject differences were found, and the Bayes Factor for the main effect of environment indicated substantial evidence for the null hypothesis (BF_{01} = 5.5). During the training phase, there were no significant effects of environment, task, or trial type on number of trials to criterion or number of guided trials. Thus, although probe objects attracted slightly more interest during exploration, the non-Euclidean environment was no more difficult to learn than the Euclidean environment.

2.3.2 Metric shortcut task

For the metric shortcut task, if primary spatial knowledge is Euclidean, shortcuts should be close to the average location of the stretched target (higher CE) and be more variable (higher mean within-subject AD) in the Elastic Maze compared to the Control Maze, and on probe trials compared to control trials (*Prediction 1*). Mean CE and AD appear in Figure 5A,B. Watson-Williams tests did not reveal any significant effects of environment or trial type on either constant (CE) or variable (VE) error ($p > .05$). Moreover, the equivalent Bayesian analysis revealed substantial evidence in favor of the null hypothesis for CE when comparing environments (BF_{01} = 4.15) and trial types (BF_{01} = 3.61). There was also substantial evidence in favor of the null hypothesis for AD in the two environments (BF_{01} = 6.02) and the two trial types (BF_{01} = 6.32). Thus, metric shortcuts were substantively the same in the Elastic and Control Mazes, and on stretched and control trials, contrary to *Prediction 1* but consistent with *Prediction 2*.

Given the high variability in metric shortcuts observed in the Control Maze (mean within-subject *AD* = 37.92˚), the estimated JNDs (*M* = 30.7˚) indicated that only one of the four

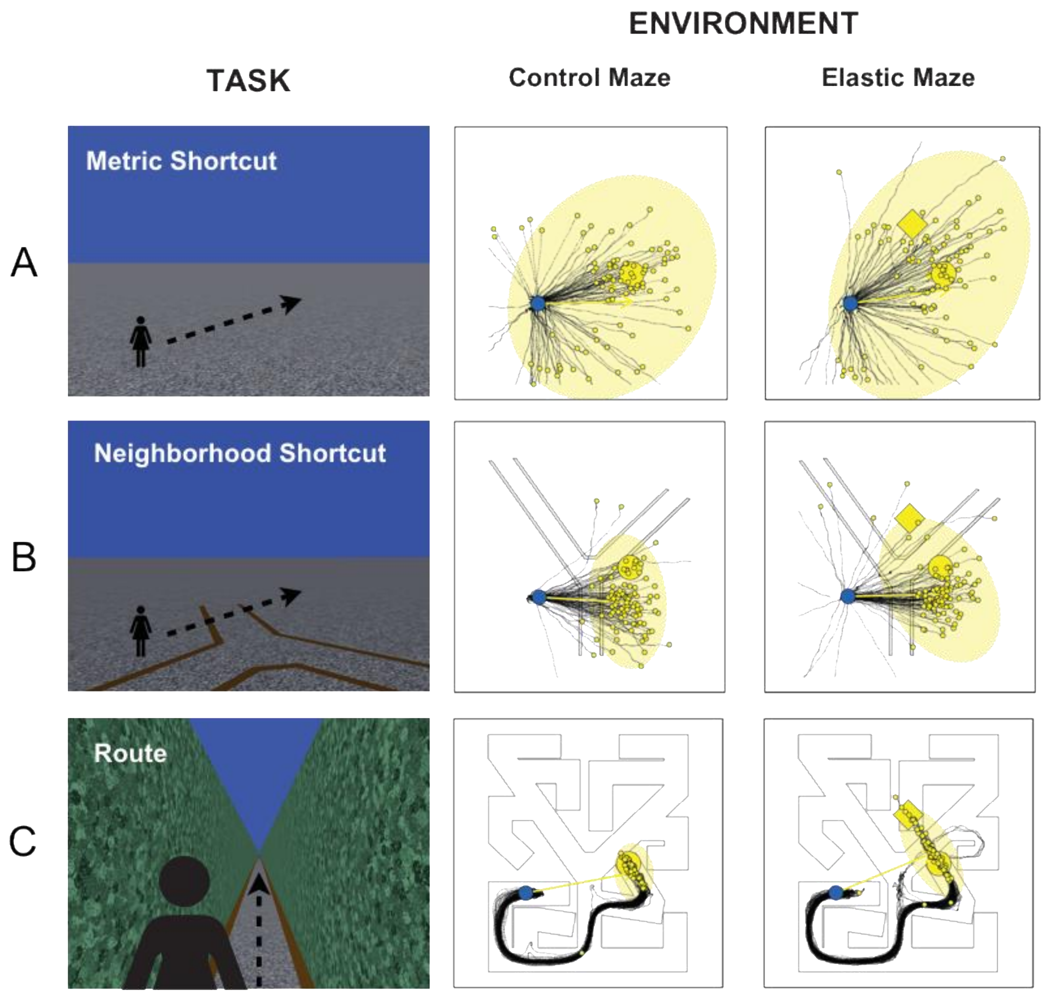

Figure 4. Experiment 1: example shortcuts (black paths) for earth (blue circle) → moon trials. (A) Metric shortcut task, (B) Neighborhood shortcut task, (C) Route task. Aggregated shortcuts for all participants are plotted in each panel. Individual shortcuts are shown as black paths radiating from the mean starting point (object A's approximate location), and small yellow dots indicate shortcut endpoints. *Canonical* and *stretched* locations of the targets represented by large yellow circles and diamonds respectively. Yellow ellipses represent 95% confidence ellipses for shortcut endpoints.

stretched targets in the Elastic Maze was detectable during learning. This implies two possibilities: (1) Euclidean knowledge is so imprecise that participants cannot discriminate locations 3m (or 30˚) apart, or (2) spatial knowledge is not Euclidean (*Prediction 2*).

2.3.4 Neighborhood shortcut task

For the Neighborhood Shortcut Task (Figure 5C), a Watson-Williams test on CE found no effect of environment ($p > .05$; $BF_{01} = 4.22$, substantial evidence for H_0). We did observe a significant main effect of trial type on CE, $F(1,46) = 8.2$, $p < .01$ ($BF_{10} = 1.46$, anecdotal evidence for H_1). However, the bias on probe trials ($M = -7.05^{\circ}$, $AD = 8.66^{\circ}$) was in the *opposite* direction of the stretched target, compared to control trials ($M = -.88^{\circ}$, $AD = 5.63^{\circ}$). In effect, neighborhood shortcuts shifted toward the center of the neighborhood in both mazes (e.g. Figure 4B), consistent with the hypothesis that objects are qualitatively localized in neighborhoods. We believe this bias was not observed on control trials because more of these objects were positioned closer to the center of their neighborhood (see Fig. 2A). Moreover, there was no effect of environment or trial type on within-subject AD (Figure 5D), and the corresponding Bayesian analysis showed substantial evidence for the null hypothesis ($BF_{01} = 3.48$ for environment; $BF_{01} = 3.03$ for trial type). Neighborhood shortcuts were thus comparable in the Elastic and Control Mazes, contrary to Euclidean hypothesis (*Prediction 3*) but consistent with the Neighborhood hypothesis (*Prediction 4*).

We also compared specific predictions of the Euclidean and Neighborhood hypotheses. Because participants did not cross a visible boundary on stretched paths during learning, the topological Neighborhood model (M_N) predicts shortcuts toward the middle of the neighborhood (to the short target location, to be conservative), with an expected CE of $\mu_N=0^{\circ}$. In contrast, because participants walked to short and long target positions during learning, the Euclidean model (M_E) predicts shortcuts, on average, to the mean target position, with an expected CE of $\mu_E=14.45^{\circ}$. The concentration parameter was $\kappa=15$, corresponding to $AD=15.30^{\circ}$ on neighborhood shortcuts in the Control Maze. The resulting $BF_{NE} >> 100$ indicated decisive evidence in favor of the Neighborhood hypothesis, and the same result is obtained for each of the four probe targets individually. These results are contrary to *Prediction 3* and support *Prediction 4*.

Because JNDs for neighborhood shortcuts in the Control Maze (*M* = 11.0˚) were smaller than the stretch angles for all four probe targets in the Elastic Maze, the stretched target was detectable during learning. Yet neighborhood shortcuts did not shift towards the stretched location in the Elastic Maze, and thus did not demonstrate sensitivity to metric neighborhoods.

The Neighborhood hypothesis also predicts that if neighborhoods are defined by visible topological boundaries (paths), neighborhood shortcuts should be less variable than metric shortcuts in the Elastic Maze (*Prediction 4*). Indeed, the mean within-subject AD for neighborhood shortcuts (*M* = 15.9º, *SD* = 9.8º) was half that for metric shortcuts (*M* = 32º, *SD* = 18.8º). The ANOVA on AD confirmed a main effect of task, $F(1,22) = 7.27$, $p < .05$, $\eta_G^2 = .23$ ($BF_{10} = 6.28$, substantial evidence for H_1). Thus, consistent with *Prediction 4*, variable error was lower for neighborhood shortcuts, indicating that neighborhoods depend upon visible topological boundaries. Watson-Williams tests on CE did not reveal any significant effects of task.

Results for the metric shortcut and neighborhood shortcut tasks are consistent with (but do not distinguish between) two possibilities: (1) Euclidean knowledge is too imprecise to support shortcuts to discriminable locations *(Prediction 2)*, or (2) neighborhoods are not derived from Euclidean relations, but topological boundaries (*Prediction 4*).

2.3.5 Route task

For the Route Task, CE on probe trials shifted toward the stretched target in the Elastic Maze (*M* = 5.73º, *AD* = 4.5º) compared to the Control Maze (*M* = -4.01º, *AD* = 3.5º) (Figure 5E). The Watson-Williams test on CE confirmed a main effect of environment, $F(1,190) = 37.4$, $p < .001$ ($BF_{10} >> 100$, decisive evidence for H_1). Results of post-hoc Watson-Williams tests

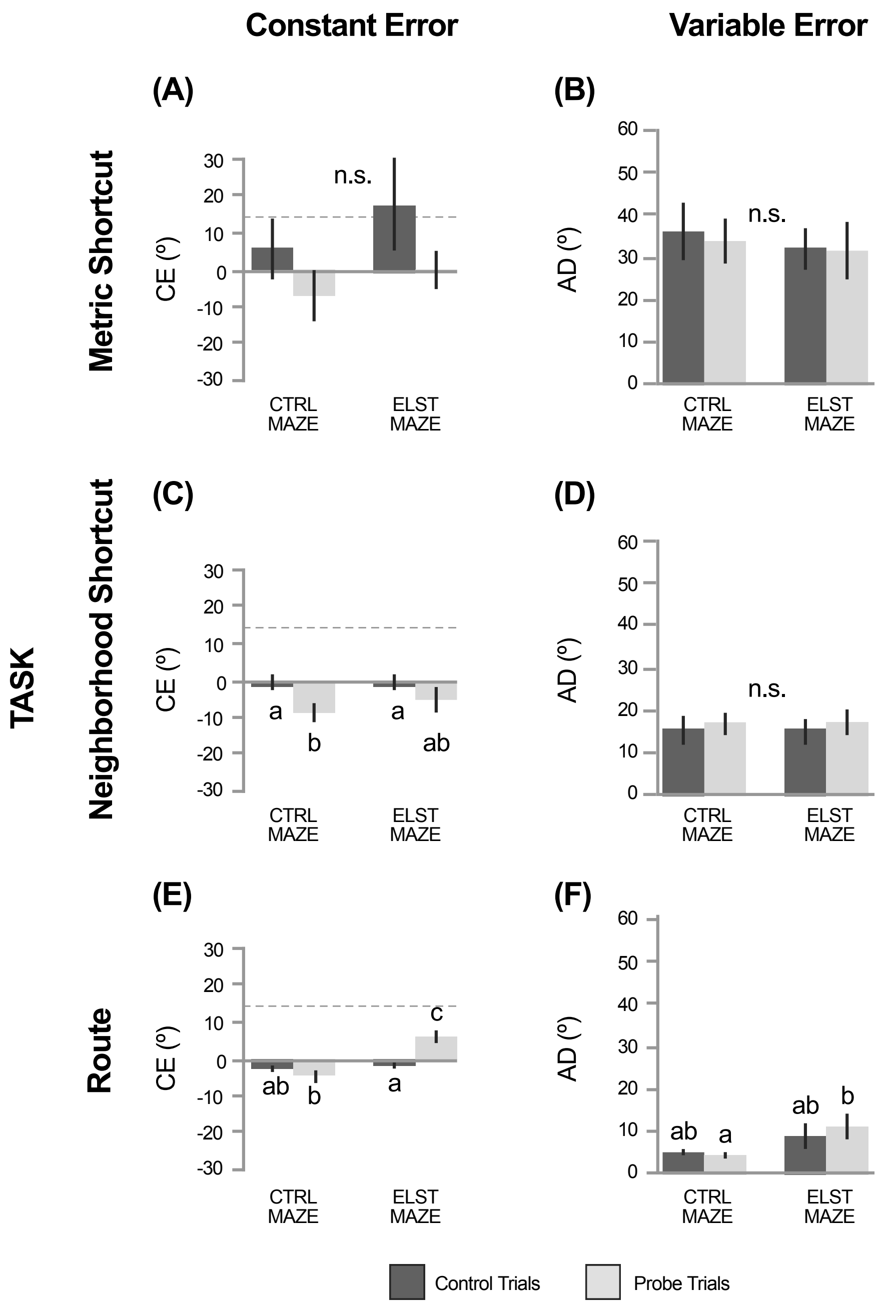

Figure 5. Experiment 1: Mean constant and variable errors. Constant errors (CE) were normalized so that 0º corresponded to perfect accuracy to the control target on control trials, or the unstretched location of the probe trial target on probe trials. Thus, for probe trials (gray bars), a positive shift in constant error indicates a shift towards the stretched location of the target. Variable errors (VE) are mean within-subject angular deviations (AD). Dotted lines indicate the average of the short and long target positions (14.45º). Error bars for CE indicate circular 95% confidence limits; error bars for VE indicate the standard error of the mean within-subject ADs. Duncan flags indicate significant ($p < .05$) post-hoc Tukey tests, and bars with the same flag were not significantly different; n.s. indicates that no significant differences were found between the four bars.

(indicated by Duncan flags in Figure 5C) also revealed a significant shift on stretched trials compared to control trials in the Elastic Maze ($p < 0.05$). Using the CE for probe targets in the Control Maze (-4.01˚) to correct for path integration error to the same targets in the Elastic maze (CE 5.73˚), we estimate the angular shift in the Elastic Maze (9.74˚) as being 67.4% of the way to the average target position (14.45º), and the corresponding Bayes factor was large (BF_{10} >> 100, decisive support for H_1).

JND analysis ($M = 3.0$˚) revealed that the all elastic targets were detectable during learning; moreover, the significant shift in CE in the Elastic Maze confirms that they were actually detected. Given the absence of any shift in the metric shortcut task, this finding is strikingly consistent with the acquisition of local information about traversed distance (edge weights in a labeled graph), but not with object coordinates in a Euclidean map. This pattern of results supports the Cognitive Graph hypothesis (*Prediction 6b*).

Variable error was higher overall in the Elastic Maze ($M = 9.74$º, $AD = 1.15$º) than in the Control Maze ($M = 4.01$º, $AD = 1.15$º). The ANOVA on within-subject AD confirmed a significant main effect of environment, $F(1,22) = 4.47$, $p < .05$, $\eta_G^2 = .16$, and a significant environment x trial type interaction, $F(1,22) = 7.32$, $p < .05$, $\eta_G^2 = .017$ (Figure 5F). The Bayesian equivalent comparing environments found substantial evidence for the alternative hypothesis ($BF_{10} = 8.45$). Thus, the route task was sensitive to the varying target position. However, an ANOVA revealed that within-subject AD for the route task ($M = 6.93$º, SD = 6.77) was significantly smaller than that for metric shortcuts ($M = 33.31$º, $SD = 18.67$), $F(1,44)= 41.5$, $p < .001$, $\eta_G^2 = .47$ (BF_{10} >> 100, decisive evidence for H_1), contrary to *Prediction 5b* and supporting *Prediction 6b*.

2.3.6 JND Analysis

Computed JNDs for the metric shortcut task were too large to conclude that the elastic target was detectable during learning. However, JNDs for both Neighborhood and Route tasks indicate that the elastic target was detectable. Given that the three groups all learned the same Elastic Maze, this strongly implies that the target was stretched far enough to be detectable in all conditions. Nevertheless, no shifts were observed in metric or neighborhood shortcuts, whereas a significant shift was found in route responses. Taken together, this implies that (a) Euclidean knowledge is too imprecise to support shortcuts to discriminable locations, (b) consequently, neither neighborhoods nor the place graph are derived from Euclidean knowledge, but (c) local path lengths (edge weights) are acquired during learning. This pattern of results is consistent with the Cognitive Graph hypothesis.

2.3.7 Bimodality

The Euclidean hypothesis predicts (*Prediction 3*) that if metric neighborhoods are derived from Euclidean structure, neighborhood shortcuts to the Moon and Gear should be more bimodal in the Elastic Maze than in the Control Maze. However, contrary to *Prediction 3,* the cluster analysis did not show stronger evidence for bimodality in the Elastic Maze than the Control Maze, and the other bimodality analyses did not indicate more than one mode for any individual target. The same was true for the metric shortcut task and the route task. These results were contrary to the Euclidean hypothesis.

2.3.8 Endpoints

The percentage of endpoints falling in each of the four possible neighborhood categories (wrong, path, short, long) was computed for the probe trials in each task. For the metric shortcut and neighborhood shortcut tasks, there were no significant differences between the Elastic and Control Mazes for any of the elastic targets in any endpoint category ($p>.05$). Bayes Factors indicated anecdotal support for the null hypothesis. Thus, we found no evidence that neighborhood boundaries influenced shortcuts. The Neighborhood hypothesis predicts (*Prediction 4*) that if neighborhoods are defined by visible topological boundaries, then more neighborhood shortcuts than metric shortcuts should end in the short neighborhood in the Elastic Maze. The mean number of endpoints falling in short neighborhoods was significantly higher for the neighborhood shortcut task (M = 83.8%, SD = 17.1%) than the metric shortcut task (M = 47%, SD = 27.9%), $F(1,22) = 15.2$, $p < .001$, $\eta_G^2 = .38$ (BF_{10} = 111.5, decisive evidence for H_1). This result is consistent with *Prediction 4* that neighborhoods are defined by visible boundaries.

In the route task, the mean percentage of endpoints falling in the short or long neighborhood shifted significantly for the two probe targets that were stretched across paths. Specifically, for the Moon, fewer endpoints fell in short neighborhood in the Elastic Maze (47.45%) than in the Control Maze (96.3%), $F(1,22) = 22.17$, $p < .001$, $\eta_G^2 = .502$ ($BF_{10} >> 100$, decisive evidence for H_1), while more fell on nearby paths, $F(1,22) = 16.70$, $p < .001$, $\eta_G^2 = .432$ ($BF_{10} >> 100$, decisive Evidence for H_1). For the Gear, fewer endpoints fell in the Short neighborhood in the Elastic Maze (27.8%) than the Control Maze (84.3%), $F(1,22) = 16.95$, $p < .05$, $\eta_G^2 = .435$ ($BF_{10} >> 100$, decisive evidence for H_1), while more fell in the Long neighborhood (30% vs 0%), $F(1,22) = 9.69$, $p < 0.01$, $\eta_G^2 = .306$ ($BF_{10} = 16.2$, strong evidence for H_1). There were no significant shifts for the Clock and the Bookcase, as overshooting the Short position would not cross into an adjacent neighborhood. These results are consistent with *Prediction 6b*, that participants learn local path lengths to the average target position.

2.3.9 Path choices

The Cognitive Graph hypothesis predicts that path selection will be correct (to the 'short' target location) in all conditions, whereas if a graph is derived from Euclidean coordinates, path choices in the Elastic Maze should be bimodal to the Moon, Bookcase, and Clock. In the route task, the percentage of correct path choices was near ceiling in both the Control (*M* = 99.8%, *SD* = 1%) and Elastic (*M* = 97.3%, *SD* = 4.4%) Mazes. ANOVAs on the number of correct and incorrect path choices found no significant differences between the Elastic and Control Mazes for any target; Bayes Factors yielded anecdotal evidence for the null hypothesis for each target. Thus, participants learned the place graph of both mazes despite the shifting positions of probe targets. These results are inconsistent with Euclidean *Prediction 5a*, but consistent with Graph *Prediction 6a*.

2.3.10 Debriefing

Detailed comparisons of debriefing results for Experiments 1 and 2 are presented in the Supplementary Material (Section 6, Comparison of Experiments). No significant differences on tests of spatial ability were found between groups, implying that the experimental results are not attributable to group differences. Three participants in the Control Maze reported thinking that some of the objects might be "overlapping" or in the same physical location despite being located down different paths. However, none of the participants in the Elastic Maze reported noticing that paths stretched.

2.4 Discussion

Table 1 summarizes the predictions for each task and the corresponding results of Experiment 1 (check-marks indicate consistent and *X*s inconsistent results). We review them here.

Predictions 1 and 2: The Euclidean hypothesis predicts that if primary spatial knowledge is Euclidean, metric shortcuts in the Elastic Maze should shift to the average target location and be more variable compared to the Control Maze; the same should be true on probe trials compared to control trials in the Elastic Maze (*Prediction 1*). Contrary to this prediction, the analyses of angular errors found that CE and VE were comparable in the two mazes, and on probe and control trials, with substantial support for the null hypothesis. These results supported Graph *Prediction 2*, that metric shortcuts are similarly unreliable in both mazes, although this could also result from Euclidean knowledge that is too imprecise to enable metric shortcuts to locations that were discriminable during learning (3m or 29˚ apart).

Prediction 3: The Euclidean hypothesis predicts that if neighborhoods are derived from Euclidean structure, neighborhood shortcuts in the Elastic Maze should be more bimodal, and more variable, than in the Control Maze, and on probe trials than on control trials. The results failed to support any of these predictions, but provided substantial evidence for the null hypothesis. Notably, we found no evidence of bimodality in any condition. The results thus contradicted *Prediction 3*.

Prediction 4: The Neighborhood hypothesis states that topological neighborhoods are defined by visible boundaries; this predicts that neighborhood shortcuts in the Elastic Maze should be unimodal and similar to those in the Control Maze, and more unimodal and less variable than metric shortcuts. The data supported these predictions. Neighborhood shortcuts were comparable in the two mazes, with substantial support for the null hypothesis. Compared to metric shortcuts, they also had smaller within-subject ADs, CEs closer to the short location, and more endpoints in the short neighborhood, with decisive support for the alternative hypothesis, providing clear evidence for *Prediction 4*. The neighborhood shortcut data thus support the topological Neighborhood hypothesis.

Predictions 5 and 6: If the graph of the environment is derived from Euclidean knowledge, path choices to the elastic target should be bimodal, because the coordinates of short and long targets fall in different corridors in the Elastic Maze, compared to the Control Maze (*Prediction 5a*). In contrast, if the graph is primary, then chosen paths should be correct and unimodal (*Prediction 6a*). Path choices in the route task were over 97% correct, and hence unimodal, in both environments, contrary to *Prediction 5a* but consistent with *Prediction 6a*.

Further, the Euclidean hypothesis predicts that CE and VE in the route task should be comparable to metric shortcuts, given that participants walk to the same target coordinates in both tasks (*Prediction 5b*). In contrast, the Cognitive Graph hypothesis predicts that CEs on the route task should shift to the average location, with smaller VE than metric shortcuts, because approximate local path lengths are learned via path integration (*Prediction 6b*). In the route task, CEs (corrected for path integration error) shifted two-thirds of the way to the average target location in the Elastic Maze, whereas the metric shortcuts showed no such effect. This was reasonably close to the expected shift, given that path integration errors are incorporated into a labeled graph. Moreover, the VE was significantly smaller than for metric shortcuts. These results are inconsistent with *Prediction 5b* but consistent with *Prediction 6b.* Participants thus acquired approximate local path lengths, but this information was not embedded in a consistent Euclidean structure.

We acknowledge that participants only spent a total of 2.5 hours in the virtual maze. It is possible that additional time learning the maze would have enabled them to acquire a Euclidean map. Nevertheless, shortcuts on control trials in the Euclidean maze were accurate on average (mean CE = 5.3º) with a large variability (mean within-subject AD = 24.4º). This level of performance is comparable to other experiments in VR (Warren et al., 2017) and to previous studies of extended learning in real environments (Ishikawa & Montello, 2006; Moeser, 1988;

Schinazi et al., 2013), suggesting that further experience is unlikely to improve shortcut performance significantly.

2.5 Conclusions

Experiment 1 reveals a pattern of results consistent with the Cognitive Graph hypothesis, which states that primary spatial knowledge can be characterized as a rough labeled graph. Metric shortcuts were reasonably accurate on average, but highly imprecise, and did not shift toward the average location of short and long targets. In contrast, endpoints in the route task were accurate, precise, and shifted towards the average target location. These results imply that spatial knowledge resembles a graph that is labeled with approximate information about local path lengths. The metric shortcut data could be explained by vector addition through a noisy graph, yielding variable shortcuts that are insensitive to moderate changes in metric structure (Warren, et al., 2017).

Highly variable metric shortcuts do not by themselves rule out Euclidean spatial knowledge, for they could also result from an imprecise metric map. However, the Euclidean hypothesis that a noisy map is the primary form of spatial knowledge cannot explain the pattern of findings in Experiment 1. Neighborhood shortcuts were more precise than metric shortcuts, and depended on visible boundaries rather than metric relations; this strongly implies that neighborhoods were not derived from imprecise Euclidean knowledge. Similarly, the route task was more accurate, more precise, and reflected local path lengths; this also implies that a labeled graph was not derived from Euclidean knowledge. The results of Experiment 1 are thus contrary to the Euclidean hypothesis, but consistent with both the Neighborhood and Graph hypotheses.

3. Experiment 2: The Swap Maze (invariant neighborhoods)

Experiment 1 varied Euclidean structure and metric neighborhoods while holding the place graph constant; the results were consistent with both the topological Neighborhood and Cognitive Graph hypotheses. The purpose of the second experiment was to dissociate these two hypotheses, and to test the Constancy hypothesis. Experiment 2 thus, conversely, varied the place graph while holding neighborhoods constant, thereby pitting them against each other. Specifically, the Swap Maze was designed to vary the nodes and edges in the graph that correspond to the same place, while preserving neighborhoods, by having pairs of objects alternate between two locations (A and B) within the same neighborhood during learning. The neighborhood shortcut and route tasks were performed in the Swap Maze, and the results were compared with the corresponding conditions in the Control Maze from Experiment 1.

According to the Neighborhood hypothesis, topological neighborhoods are defined by visible boundaries, such as the Y-shaped skeleton of the virtual maze (Figure 6). For example, the Clock place and the Flamingo place both lie between the left and right paths, and hence fall in the same constant neighborhood. Neighborhood shortcuts to these targets should thus be equally successful in the Swap and Control Mazes. In the route task, if neighborhoods are primary, participants should take any path that leads to the neighborhood containing the swapped targets, so the chosen path would be expected to vary.

According to the Cognitive Graph hypothesis, neighborhood relations are derived from the place graph, where places are defined by salient objects. In Figure 6A, for example, one neighborhood lies to the right of the edge leading to the Clock place and to the left of the edge leading to the Flamingo place; this neighborhood contains the Flamingo. In the Swap Maze, however, the Clock and the Flamingo switch locations, so two different edges lead to the Clock place. Hence, "right of the edge leading to the Clock" defines two different neighborhoods, only one of them containing the Flamingo (Figure 6B). This renders neighborhood boundaries inconsistent, so neighborhood shortcuts should be more unreliable in the Swap Maze than the Control Maze. For the route task, path choices to the Clock should be unimodal in the Control Maze (to node A) but bimodal in the Swap Maze (to nodes A and B). Consequently, estimates of target position should be more variable in the Swap Maze, and may fall outside the correct neighborhood, because they are based on local path lengths in two different corridors.

Finally, according to the Constancy hypothesis, spatial knowledge preserves whatever geometric properties remain invariant during learning. Because neighborhoods defined by the Y-shaped skeleton are constant in the Swap Maze, predictions are the same as for the Neighborhood hypothesis: neighborhood shortcuts should be successful, and participants should choose varying paths that all lead to the neighborhood containing the swapped targets.

3.1 Predictions

These hypotheses lead to specific predictions for the two tasks (refer to Table 1).

3.1.2 Neighborhood shortcut task

Prediction 7: If Neighborhood knowledge is primary, or spatial knowledge preserves constant geometric properties, neighborhood shortcuts should be (7*a*) similar in the Swap and Control Mazes, and (7*b*) their endpoints should fall within the neighborhood containing the two swapped targets, in both mazes. *Prediction 8*: If neighborhood relations are derived from the place graph, neighborhood shortcuts in the Swap Maze should (8*a*) be less accurate or more variable than in the Control Maze, and (8*b*) more shortcut endpoints may fall outside of the correct neighborhood than in the Control Maze.

3.1.3 Route task

Prediction 9: If neighborhood knowledge is primary, or spatial knowledge preserves constant properties, participants should choose any path that leads to the neighborhood that contained the two swapped targets during learning, so the chosen path would be expected to vary. *Prediction 10*: If graph knowledge is primary, (10*a*) path choices should be bimodal (to the swapped nodes) in the Swap Maze, but unimodal in the Control Maze, and consequently (10*b*) estimates of target position based on local path lengths should be more variable in the Swap Maze, and may fall outside the correct neighborhood.

3.2 Method

3.2.1 Participants

A total of 24 (12M, 12F) new participants were run the in the two Swap Maze conditions. Each group consisted of 12 participants (6M, 6F), and the mean age of participants who completed the study was 20.8 (*SD* = 3.2). One participant was dropped from the Swap / Route condition due to symptoms of simulator sickness.

3.2.2 Design

Including the two groups in the Swap Maze (Experiment 2) and the two corresponding groups in the Control Maze (from Experiment 1), this yielded a 2 x 2 x 2 design, with two environments (Control Maze, Swap Maze) in the learning phase crossed with two navigation tasks (Neighborhood Shortcut, Route) and two trial types (Probe, Control) in the test phase. Environment and task were between-subjects factors, and trial type was a within-subject factor. Each participant experienced only one virtual environment and one response task, and trial order was randomized for each participant.

3.2.3 Displays

The Swap Maze was identical to the Control Maze except that pairs of probe objects (bookcase/gear; clock/flamingo) switched locations repeatedly during the free exploration and training phases (Figure 6). The initial position of each object was randomized between participants. For example, the first time a participant walked down the canonical path for the

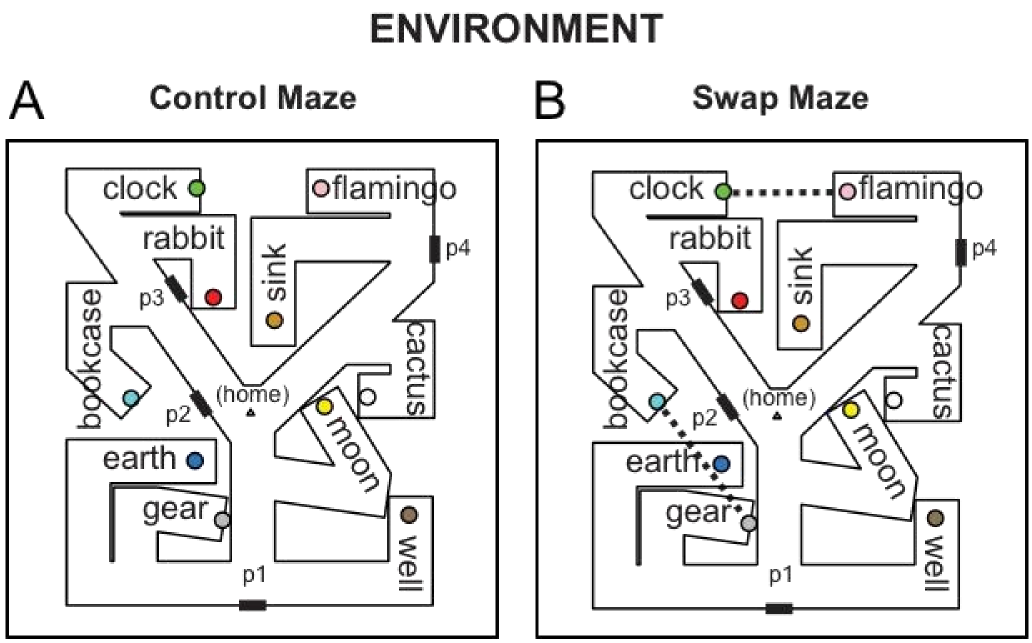

Figure 6. Experiment 2: mazes. (A) The layout of the Control Maze was the same as before. (B) The Swap Maze was identical to the Control Maze except that pairs of probe objects (bookcase/gear; clock/flamingo) exchanged locations repeatedly during free exploration and training phases.

flamingo, they would see the flamingo; the next time they walked down the same path, they would see the clock; next, they would see the flamingo; and so on. If participants walked to the incorrect path when trying to find an object during the training phase, they were guided to the alternative location for that object. This was done to ensure that participants would learn that a given object could appear in multiple locations, rather than learning that multiple objects appear in a particular location. Thus, in the Swap Maze a particular path could lead to two different "places" as defined by the objects.

3.2.4 Procedure

The procedure in Experiment 2 was the same as before, except for the training phase, which was modified based on pilot testing that showed some participants were not able to reach the training criterion in the Swap Maze. To reduce attrition and ensure sufficient data in the test phase, participants in the Swap Mazes continued to the test phase after 25 min of training, even if they had not met the criterion of finding each object within 30 s. The number of training trials required to reach the criterion (or before 25 min had elapsed) were counted to assess how difficult it was for participants to learn the Swap Maze.

3.2.5 Data analysis

The analysis was the same as before, except that probe objects in the Swap Maze were the clock, flamingo, gear, and bookcase, and control objects were the moon, well, earth, cactus, rabbit, sink. Therefore, objects in the Control Maze from Experiment 1 were re-coded to match their control/probe designations in the Swap Maze, for statistical comparisons. For Neighborhood shortcut and Route tasks, CEs on probe trials were normalized so that 0º corresponded to walking toward the canonical location (A) and positive values corresponded to walking in the direction of the swapped target location (B), in this case toward the middle of the neighborhood; and endpoints were classified as falling within the correct neighborhood (containing the A/B locations of the swapped targets), the wrong neighborhood, or on paths (Figure 7A). For the Route task, path choices were classified as correct if paths terminated in the correct neighborhood, and at either the canonical (A) or swapped (B) target location; path choices were classified as wrong if they terminated in any other hallway (Figure 7B).

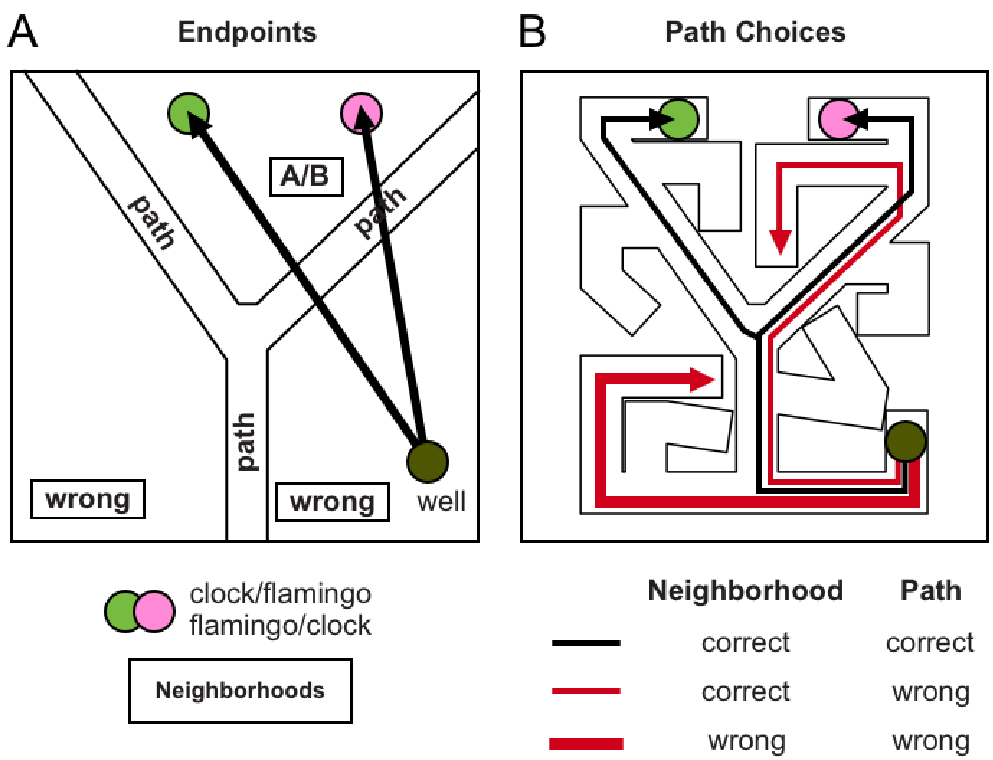

Figure 7. Experiment 2: classification scheme for endpoints and path choices. (A) Percentages of endpoints falling in each of the three possible neighborhoods (A/B, paths, wrong) were computed for each participant. (B) Wrong path choices were further subdivided into paths to objects located in the wrong neighborhood (thick red line), and non-A/B paths in the same neighborhood as the A/B target (thin red line).

3.3 Results

3.3.1 Free exploration phase

No statistically significant differences between groups were found, suggesting that participants explored Control and Swap Mazes to similar extents.

3.3.2 Training phase

Participants required more training trials per object in the Swap Maze (M = 5.2, SD = 1.1) than in the Control Maze (M = 4.2, SD = 0.4) to reach criterion (or before 25 min had elapsed),

$F(1,44) = 27.1$, $p < .001$, $\eta_G^2 = .12$ ($BF_{10} >> 100$, decisive evidence for H_1). This implies that the Swap Maze was harder to learn than the Control Maze.

3.3.3 Neighborhood shortcut task

Sample neighborhood shortcuts appear in Figure 8A, and mean constant and variable errors in Figure 9A and 9B respectively. Watson-Williams tests on CE did not find any main effects of environment or trial type. Pairwise post-hoc Watson-Williams tests revealed that, in the Swap Maze, CE was significantly more negative on control trials (M = -17.3, AD = 25º) than

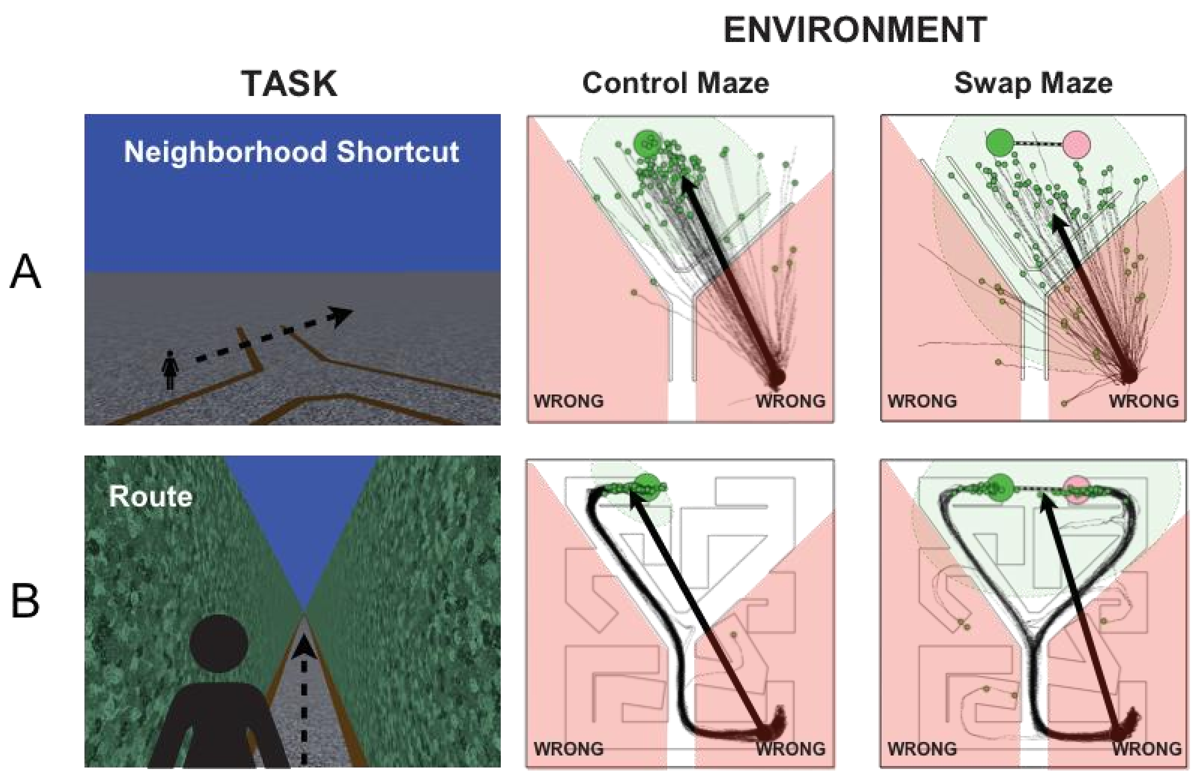

Figure 8. Experiment 2: example shortcuts (black paths) for well (blue circle) → clock/flamingo (green/pink circles) large trials. (A) Neighborhood shortcut task, (B) Route task. Aggregated shortcuts for all participants are plotted in each panel. Individual shortcuts are shown as black paths originating at the mean starting point (object A's approximate location), and small green dots indicate shortcut endpoints. Swapped locations of the targets represented by large (green and pink) circles linked by checkered lines. Green ellipses represent 95% confidence ellipses for shortcut endpoints.

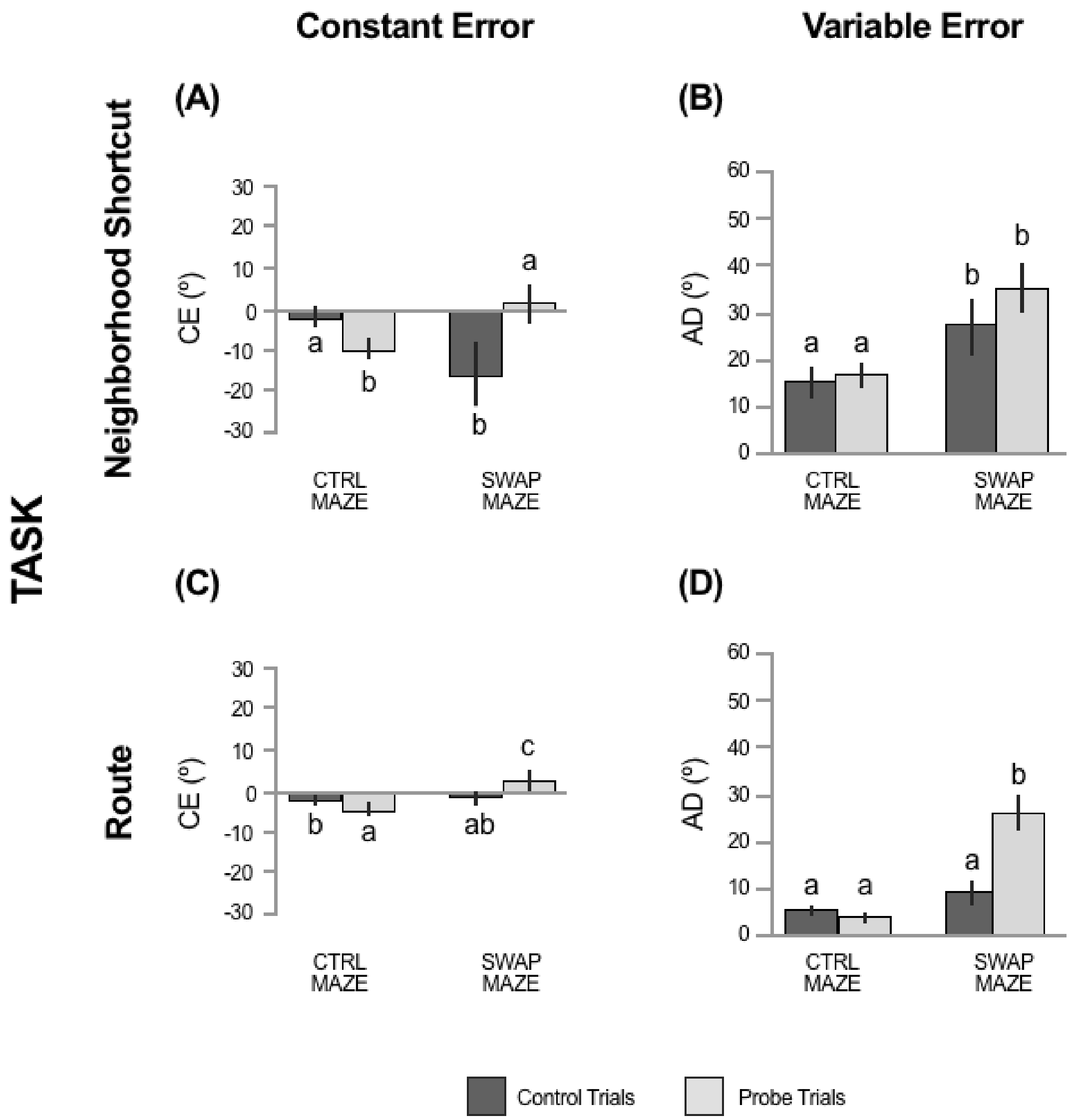

Figure 9. Experiment 2: Mean constant errors (CE) and variable errors (within-subject angular deviations, AD). Constant errors were normalized so that 0º corresponded to perfect accuracy to the control target on control trials, or the A location of the swapped target on probe trials. Thus, for probe trials, a positive shift in angular error indicates a shift towards the B location of swapped targets. Error bars and Duncan flags (p < .05) are the same as in Figure 5.

on probe trials ($M = 2.11º$, $AD = 13.8º$), indicating a bias toward the edge of the neighborhood (see Duncan flags in Figure 9A); there is no apparent reason why this was the case. Variable Errors, on the other hand, were larger in the Swap Maze than in the Control Maze Figure 9B. The ANOVA on mean within-subject AD revealed a main effect of environment,

$F(1,22) = 7.81$, $p < .05$, $\eta_G^2 = .25$ ($BF_{10} = 7.8$, substantial evidence for H_1), a main effect of trial type, $F(1,22) = 8.22$, $p < .01$, $\eta_G^2 = .03$, and an environment x trial type interaction, $F(1,22) = 4.45$, $p < .05$, $\eta_G^2 = .016$ ($BF_{10} = 9.2$, substantial evidence for H_1). Post- hoc Tukey tests revealed that mean AD was approximately twice as large in the Swap Maze (*M* = 30.9º, *SD* = 5.7º) as in the Control Maze (*M* = 16º, *SD* = 1.15º), but did not confirm the interaction (see Duncan flags in Figure 9B). These results are contrary to *Prediction 7a*, but consistent with *Prediction 8a:* neighborhood shortcuts were more variable in the Swap Maze than the Control Maze, suggesting that neighborhoods are derived from the varying place graph. The significant interaction indicates that VE may be greater for swapped targets than control targets.

3.3.4 Route task

Sample route task shortcuts appear in Figure 8B, and mean constant and variable errors in Figure 9C and 9D respectively. For the Route Task, the Watson-Williams tests on CE (Figure 9C) revealed a small but significant main effect of environment, such that target position was slightly underestimated in the Control Maze (*M* = -3.12º, *AD* = 2.73º) compared to the Swap Maze (*M* = .31º, *AD* = 5.9º), $F(1,46) = 6.37$, $p < .05$ ($BF_{10} = 3.2$, substantial evidence for H_1). No other significant effects were found. Results of post-hoc Watson-Williams tests appear as Duncan flags in Figure 9C.

The VE in estimated target position (Figure 9D) was significantly higher on probe trials in the Swap Maze (*M* = 25.5º, *SD* = 11.75º) than in any other condition. There was a main effect of environment $F(1,22) = 39.7$, $p < .001$, $\eta_G^2 = .46$ ($BF_{10} >> 100$, decisive evidence for H_1), a main effect of trial type, $F(1,22) = 13.5$, $p < .01$, $\eta_G^2 = .25$, and a significant interaction, $F(1,22) = 18.3$, $p < .001$, $\eta_G^2 = .31$ ($BF_{10} = 63.6$, very strong evidence for H_1). The interaction was confirmed by post-hoc Tukey tests (see Duncan flags in Figure 9D). This finding is consistent with *Prediction 10b*, for position estimates are based on local path lengths that lead to two different endpoints (Figure 8).

3.3.5 Endpoints

Neighborhood shortcuts. For the neighborhood shortcuts, the mean number of endpoints falling in correct (A/B) neighborhoods dropped from 85.8% (*SD* = 14.1%) in the Control Maze to 67% (*SD* = 32.9%) in the Swap Maze, and the SD doubled. Specifically, there were fewer correct endpoints on probe trials in the Swap Maze (*M* = 64.7%, *SD* = 33.9%) than the Control Maze (*M* = 88.3%, *SD* = 14.9%), and somewhat fewer on control trials in the Swap Maze (*M* = 69.3%, *SD* = 32.8%) than in the Control Maze (*M* = 83.3%, *SD* = 14.1%). The corresponding ANOVA indicated a marginally significant main effect of environment, $F(1,22) = 3.32$, p = .082, $\eta_G^2 = .128$, but the Bayes factor indicated substantial evidence for the alternative hypothesis ($BF_{10} = 5.39$). The ANOVA also indicated a significant environment x trial type interaction, $F(1,22) = 6.89$, $p < .05$, $\eta_G^2 = .01$ ($BF_{10} = 1.14$, anecdotal evidence for the H_1). Post hoc Tukey tests only confirmed the main effect of environment ($p < .05$).

Conversely, more endpoints fell into the wrong neighborhood in the Swap Maze (*M* = 24.1%, *SD* = 24%) than the Control Maze (*M* = 9.1%, *SD* = 10.5%), and again the SD doubled. Specifically, on probe trials there were more endpoints in the wrong neighborhood in the Swap Maze (*M* = 25.9%, *SD* = 25.5%) than the Control Maze (*M* = 6.9%, *SD* = 8.2%), as well as more on control trials in the Swap Maze (*M* = 22.3%, *SD* = 23.1%) than the Control Maze (*M* = 11.5%, *SD* = 13.2%). The corresponding ANOVA revealed a marginally significant main effect of environment, $F(1,22) = 3.86$, $p = .062$, $\eta_G^2 = .145$, but the Bayes factor indicated substantial evidence for the alternative hypothesis ($BF_{10} = 5.78$). There was also a significant environment x trial type interaction, $F(1,22) = 7.4$, $p < .05$, $\eta_G^2 = .012$ ($BF_{10} = 1.66$, anecdotal evidence for the H_1). Post hoc Tukey tests only confirmed the main effect of environment ($p < .01$).

This pattern of results suggests that varying the edges and nodes in the graph destabilized the neighborhoods of all objects, not only probe objects. Overall, neighborhood shortcuts support the hypothesis that neighborhoods are derived from the place graph (*Prediction 8b*), and are inconsistent with the Constancy hypothesis (*Prediction 7*).

Route task. In the Route Task, over 90% of the endpoints fell in the correct (A/B) neighborhood in all conditions. Nevertheless, consistent with *Prediction 10b*, more endpoints fell in the wrong neighborhood on probe trials in the Swap Maze ($M = 8.7\%$, $SD = 10.1\%$) than on control trials in that maze ($M = 2.5\%$, $SD = 4.4\%$), or on probe trials ($M = 0\%$, $SD = 0\%$) or control trials ($M = 0.4\%$, $SD = 1.1\%$) in the Control Maze. The corresponding ANOVA on endpoints in the wrong neighborhood revealed a significant main effect of environment, $F(1,22) = 8.54$, $p < .01$, $\eta_G^2 = .206$ ($BF_{10} = 14.1$, strong evidence for H_1), a significant main effect of trial type, $F(1,22) = 6.98$ ($BF_{10} = 1.22$, anecdotal evidence for H_1), $p < 0.05$, $\eta_G^2 = .095$, and a significant interaction, $F(1,22) = 5.12$, $p < 0.05$, $\eta_G^2 = .071$ ($BF_{10} = 23.2$, strong evidence for H_1). Post hoc Tukey tests revealed that probe trials in the Swap Maze had significantly more neighborhood errors than the other three conditions ($p < .05$). This finding is consistent with the Cognitive Graph hypothesis that target position estimates are based on local path lengths corresponding to edge weights in a place graph (*Prediction 10b*), and inconsistent with the Constancy hypothesis that they are based on constant neighborhood boundaries (*Prediction 7*).

3.3.6 Path choices

In the Control Maze, path choices were unimodal on both probe and control trials, with participants taking the correct path to the canonical target location (A) on 100% of control trials and 99.8% of probe trials (*SD* = 0.8%). In the Swap Maze, on the other hand, path choices to the probe target were bimodal, with paths to the canonical location (A) on 36.7% (*SD* = 21.7%) of trials and paths to the non-canonical location (B) on 54.1% (SD = 20.8%) of trials; in contrast, path choices to control targets were unimodal, with 96.3% (*SD* = 6.6%) to the canonical location (A) and 0% to location B. ANOVAs confirmed that the path to the canonical location (A) was chosen less often on probe trials than on control trials in the Swap Maze, $F(1,11) = 74.8$, $p < .001$, $\eta_G^2 = .79$ ($BF_{10} >> 100$, decisive evidence for H_1). Conversely, the path to the non-canonical location (B) was chosen more often on probe trials than control trials, $F(1,11) = 81.4$, $p < .001$, $\eta_G^2 = .88$ ($BF_{10} >> 100$, decisive evidence for H_1). Participants thus acquired a place graph despite varying node and edge assignments; moreover, they learned the two different edges that led to the same place, consistent with the Cognitive Graph hypothesis (*Prediction 10a*).

Contrary to the Neighborhood and Constancy hypotheses (*Prediction 9*), participants in the Swap Maze never took other (non-A/B) paths leading to the correct neighborhood on probe trials, yet they chose paths to the wrong neighborhood on 8.25% (*SD* = 10.7%) of these trials, despite the fact that the swapped targets remained in the same neighborhood. This percentage was significantly higher than control trials in the Swap Maze (*M* = 1.56%, *SD* = 3.88%), $F(1,11) = 6.77$, $p < .05$, $\eta_G^2 = .16$ ($BF_{10} = 5.13$, substantial evidence for H_1). In the Control Maze, paths to the wrong neighborhood were never chosen on probe trials.

In sum, despite constant neighborhoods, participants failed to take alternative paths to the correct neighborhood, and took paths to the wrong neighborhood on a significant number of trials. Yet they acquired a place graph of the maze, even with swapping nodes and edges. The pattern of results is contrary to both the Neighborhood and Constancy hypotheses (*Prediction 9*), but consistent with the Cognitive Graph hypothesis (*Predictions 8 and 10*).

3.3.7 Response Time

The ANOVAs on mean response time found no significant effects of environment ($p >$ .05; $BF_{01} = 0.59$, no evidence for H_0) or trial type ($p > .05$; $BF_{01} = 3.4$, substantial evidence for H_0).

3.3.8 Debriefing responses

Detailed comparisons of debriefing results for Experiments 1 and 2 are presented in the Supplementary Material (Section 6, Comparison of Experiments). All Swap Maze participants reported noticing that some of the objects were swapping with one another, variously describing the pattern as the objects “changing,” “alternating,” “switching,” “swapping.” All participants reported noticing the outlines of the major paths superimposed on the ground plane during shortcuts.

3.4 Discussion

The four hypotheses and their predictions for each task in Experiment 2 are summarized in Table 1, together with the experimental outcome (rightmost column). Let us walk through the predictions and results.

For the neighborhood shortcut task, both the Constancy and Neighborhood hypotheses predicted that (*Prediction 7a*) shortcuts should be comparable in the Swap and Control Mazes, and (*Prediction 7b*) their endpoints should fall within the neighborhood containing the swapped targets, because visible neighborhood boundaries (the Y-shaped skeleton) were constant during learning. Conversely, the Cognitive Graph hypothesis predicted that if neighborhoods are derived from the place graph, neighborhood shortcuts should be (*Prediction 8a*) less accurate or more variable in the Swap Maze than the Control Maze, and (*Prediction 8b*) endpoints may fall outside the constant neighborhoods.

The results indicated that the VE of neighborhood shortcuts was significantly greater in the Swap Maze, especially for swapped targets, as predicted by the Cognitive Graph hypothesis. Moreover, there was substantial evidence that fewer shortcut endpoints fell in the correct neighborhood, and more fell in the wrong neighborhood, in the Swap Maze than the Control Maze, contrary to the Neighborhood and Constancy hypotheses. Despite a significant environment by trial type interaction, post-hoc tests only supported the main effect, suggesting that varying node and edge assignments in the graph destabilized neighborhood boundaries for all target objects. This pattern of results supports the hypothesis that neighborhoods are derived from the place graph.

For the Route Task, both the Neighborhood and Constancy hypotheses predicted that (*Prediction 9*) participants should take any path leading to the neighborhood that contained the target, in both the Swap and Control Mazes, because neighborhoods were constant during learning. In contrast, the Cognitive Graph hypothesis predicted that (*Prediction 10a*) path choice should be unimodal (to A) in the Control Maze and on control trials, but bimodal (to A and B) on probe trials in the Swap Maze, given that graph knowledge is composed of edges (paths) to nodes (places). Consequently, *(Prediction 10b)* the final estimated target position should be more variable on probe trials in the Swap Maze, because local path lengths yield two different endpoints (Figure 8); they may also fall outside the neighborhood containing the target.

We found that path choices were overwhelmingly unimodal (99.8% to correct path A) in the Control Maze and bimodal (36.7% to A and 54.1% to B) on probe trials in the Swap Maze, consistent with the Cognitive Graph hypothesis. Despite constant neighborhoods, participants never took alternative paths to the correct neighborhood, but occasionally took paths to the wrong neighborhood on probe trials in the Swap Maze. Similarly, more route endpoints fell into the wrong neighborhood on those trials than in any other condition. Finally, estimated target positions were also more variable on those trials, consistent with local information about path length. This pattern of results contradicts the Neighborhood and Constancy hypotheses, but supports the Cognitive Graph hypothesis.

Overall, when the graph was varied, the environment was more difficult to learn: more training trials were required to reach criterion, and more guidance to targets was needed, in the Swap Maze than the Control Maze. Nevertheless, participants still acquired reliable graph knowledge, choosing a correct path on 93.6% of trials in the Swap Maze. In contrast, VEs and endpoint errors indicate that participants did not learn constant neighborhoods defined by the Y-shaped skeleton. Rather, the results strongly imply that neighborhoods are derived from nodes and edges in the place graph.

3.5 Conclusions

The results of Experiment 2 provide support for the Cognitive Graph hypothesis but militate against the Neighborhood and Constancy hypotheses. Graph structure appears to be the primary form of spatial knowledge: an environment in which the place graph varies is more difficult to learn and interferes with the acquisition of neighborhoods. Despite this variation, participants were able to learn that two different edges lead to the same place and acquired a reliable place graph. Conversely, despite a constant skeleton of visible paths, participants did not learn stable neighborhoods, but derived them from the place graph. These results converge with those of Experiment 1 to support the hypothesis that primary spatial knowledge is best described as a labeled place graph.

4. General Discussion

The present study examined the geometric structure of spatial knowledge by evaluating four main hypotheses: the Euclidean hypothesis, which posits that spatial knowledge corresponds to a metric map; the Neighborhood hypothesis, which proposes that it consists of adjacency relations among spatial regions; the Cognitive Graph hypothesis, which states that it is characterized by a labeled place graph; and the Constancy hypothesis, which posits that it preserves whatever geometric properties are invariant during learning.

To test these hypotheses and identify the primary form of spatial knowledge, we selectively varied three geometric properties during learning: metric relations, metric neighborhoods, and the place graph. The Elastic Maze varied metric structure while holding the place graph constant; the Swap Maze varied graph structure while holding neighborhoods constant; and the Control Maze preserved all three properties. We asked participants to learn one of these environments and then perform a navigation task that assessed their metric, neighborhood, and graph knowledge.

Table 1

Summary: Summary of predictions and results

Task	Hypothesis	Experiment	Prediction		Results	BF
Metric Shortcut	**Euclidean** Primary spatial knowledge is Euclidean	1	1	Metric shortcuts in the Elastic Maze should shift to the average target location, and be more variable, compared to the Control Maze; same on probe compared to control trials.	✖	$BF_{01} = 4.15$ $BF_{01} = 3.61$ $BF_{01} = 6.02$ $BF_{01} = 6.32$
	Cognitive Graph Primary spatial knowledge resembles a rough labeled place graph (or is highly imprecise)	1	2	Metric shortcuts should be directional but similarly unreliable in the Elastic and Control Mazes, and on probe and control trials	✓	Same
Neighborhood Shortcut	**Euclidean** Neighborhoods are derived from metric relations between places and boundaries	1	3	Neighborhood shortcuts to stretched targets should be bimodal and more variable in the Elastic Maze than in the Control Maze; and on probe trials than control trials	✖	$BF_{01} = 4.22$ $BF_{01} = 3.48$ $BF_{01} = 3.03$ $BF_{NE} >> 100$

	Neighborhood Primary spatial knowledge consists of topological neighborhood relations	1	4	Neighborhood shortcuts in the Elastic Maze should be similar to the Control Maze; less variable than metric shortcuts, with more endpoints in the short neighborhood	✓	Same $BF_{10} = 6.28$ $BF_{10} = 111.5$
	Cognitive Graph Neighborhood relations are derived from the place graph	1	4	Same	✓	Same
	Constancy Spatial knowledge preserves whatever geometric properties remain constant	2	7a	Neighborhood shortcuts should be comparable in the Swap and Control Mazes	✖	$BF_{10} = 5.39$ $BF_{10} = 1.14$ $BF_{10} = 5.78$ $BF_{10} = 1.66$
		2	7b	Shortcut endpoints should fall within the neighborhood containing the swapped targets, in the Swap and Control Mazes	✖	$BF_{10} >> 100$ $BF_{10} >> 100$ $BF_{10} >> 100$ $BF_{10} = 16.2$
	Neighborhood Primary spatial knowledge consists of topological neighborhood relations	2	7a,b	Same	✖	Same
	Cognitive Graph Neighborhood relations are derived from the place graph	2	8a	Neighborhood shortcuts in the Swap Maze should be less accurate or more variable than in the Control Maze	✓	$BF_{10} = 7.8$ $BF_{10} = 9.2$
		2	8b	Shortcut endpoints in the Swap Maze may fall outside the correct neighborhood more than in the Control Maze	✓	$BF_{10} = 5.39$ $BF_{10} = 1.14$ $BF_{10} = 5.78$ $BF_{10} = 1.66$
Route	**Euclidean** Graph knowledge is derived from metric relations among places and paths	1	5a	Path choice should be bimodal in the Elastic Maze because short and long targets fall on different paths	✖	>97% correct (unimodal)
		1	5b	Estimated target positions should be similar to metric shortcuts to the same targets	✖	$BF_{10} >> 100$ $BF_{10} = 8.45$
	Cognitive Graph Primary spatial knowledge resembles a rough labeled place graph	1	6a	Path choice should be unimodal and correct in the Elastic and Control Mazes,	✓	>97% correct (unimodal)
		1	6b	Position estimates in the Elastic Maze should shift to the average target location compared to the Control Maze, and be less variable than metric shortcuts.	✓	$BF_{10} >> 100$ $BF_{10} = 8.45$
	Constancy Spatial knowledge preserves whatever geometric properties remain constant	2	9	Path choice should vary but lead to the neighborhood that contained the swapped targets the Swap and Control mazes	✖	$BF_{10} = 5.13$
	Neighborhood Primary spatial knowledge consists of topological neighborhood relations	2	9	Same	✖	Same
	Cognitive Graph Primary spatial knowledge resembles a labeled place graph	2	10a	Path choice should be bimodal in the Swap Maze, but unimodal in the Control Maze and on control trials	✓	$BF_{10} >> 100$ $BF_{10} >> 100$
	Neighborhood relations are derived from the place graph	2	10b	Estimated target position should be more variable in the Swap Maze and may fall outside the correct neighborhood	✓	$BF_{10} >> 100$ $BF_{10} = 63.6$ $BF_{10} = 14.1$

Note: ✓ indicates that results were consistent with the hypothesis. ✖ indicates that results were inconsistent with the hypothesis. "BF" indicates Bayes Factor(s) (strength of evidence favoring the corresponding result); BFs following checks and crosses support acceptance or rejection of the corresponding hypothesis respectively.

The overarching predictions for each of the four hypotheses were as follows: (1) The Euclidean hypothesis predicts that performance on all three tasks should be higher when metric structure is constant (Control Maze) than when it is varied (Elastic Maze), because geometrically weaker forms of knowledge are derived from metric spatial knowledge. (2) The Neighborhood hypothesis predicts that performance on neighborhood shortcuts should be higher when neighborhoods are constant (Swap Maze and Control Maze) than when they are varied (Elastic Maze). (3) The Cognitive Graph hypothesis predicts that performance on the route task should be higher when the place graph is constant (Elastic Maze and Control Maze) that when it is varied (Swap Maze). (4) The Constancy hypothesis predicts that participants will acquire whatever geometric properties are constant during learning, and thus perform best on metric shortcuts in the Control Maze, the route task in the Elastic Maze, and neighborhood shortcuts in the Swap Maze.

Experiment 1 compared the Control Maze and Elastic Maze. The results were generally consistent with the Cognitive Graph hypothesis. Even though we varied metric structure in the Elastic Maze, metric shortcuts were highly imprecise in both mazes, and did not shift in the direction of stretched targets even though they were detectable. This suggests two possibilities: (1) spatial knowledge is Euclidean, but too imprecise to support metric shortcuts to discriminable locations, or (2) spatial knowledge is non-Euclidean, and best described as a labeled graph. Unreliable shortcuts alone do not rule out Euclidean spatial knowledge, for they could result from an imprecise metric map. However, such an imprecise map cannot be the basis for the neighborhood and graph knowledge required to explain reliable performance in the neighborhood shortcut and route tasks.

The route task revealed that participants acquired a labeled place graph. They chose the correct path to the target on over 97% of test trials in the Elastic Maze, despite varying Euclidean structure. In addition, they walked down the path to the approximate target position, demonstrating knowledge of local metric path lengths, corresponding to edge weights in the graph. Participants also learned neighborhoods based on visible boundaries (e.g. paths and intersections): neighborhood shortcuts were unimodal and less variable than metric shortcuts in both the Control and Elastic Maze. Moreover, route endpoints were unimodal and clustered in the near neighborhood, implying that neighborhoods are based on topological boundaries, not derived from metric relations. This pattern of results is consistent with the Cognitive Graph hypothesis, in which a labeled graph (Figure 1B) incorporates local information about path lengths (edge weights).

Experiment 2 was designed to provide a clear test of the Graph, Neighborhood, and Constancy hypotheses, by varying the place graph in the Swap Maze while holding neighborhoods constant. Even though the neighborhoods bounded by the skeleton of primary paths were constant, participants had difficulty learning them when the node and edge assignments in the graph were bistable. Neighborhood shortcuts were more variable, and more shortcut endpoints fell in the wrong neighborhood, in the Swap Maze than the Control Maze. Nevertheless, participants still chose the correct path to the (A/B) target on over 96% of test trials in the Swap Maze. They thus learned the graph of the Swap Maze, including bistable edges and nodes, despite this variation. These results strongly support the Cognitive Graph hypothesis. In contrast, they are inconsistent with the Neighborhood and Constancy hypotheses, for participants were less successful at acquiring neighborhoods in the Swap Maze, even though they were constant during learning.

Taken together, the results of Experiments 1 and 2 are contrary to the Euclidean, Neighborhood, and Constancy hypotheses, but support the Cognitive Graph hypothesis. A place graph was acquired in all environments, even when we attempted to vary it in the Swap Maze. Neighborhoods were also learned, but their boundaries were derived from the place graph. Thus, primary spatial knowledge resembles a labeled place graph (Figure 1B) which incorporates local information about approximate path lengths and junction angles.

One objection to a labeled graph is that the spatial knowledge acquired in these experiments is also consistent with distorted Euclidean knowledge. However, in other experiments we have found that spatial knowledge violates the metric postulates, but is consistent with a labeled graph (Warren et al., 2017; Strickrodt, et al., 2020). Although these findings imply that 'navigation space' is non-Euclidean, it remains possible that spatial knowledge is locally Euclidean within 'vista space' (Meilinger, 2008; but see Warren, 2020). The present results are also compatible with the proposal that spatial knowledge has a hierarchical organization (Hirtle & Jonides, 1985; Montello, 1992), or that it is characterized by different spatial scales (Anooshian, 1996; Montello, 1992). We propose that a labeled graph structure provides the best description of knowledge at each level or scale.

Finally, we note that the present study was not designed to assess individual differences in primary spatial knowledge (Weisberg, et al, 2014). We hope that the 'impossible world' paradigm offers a useful method for testing specific hypotheses about the geometry of spatial knowledge in a larger subject population.

5. Conclusion

The present study critically examined the structure of human spatial knowledge by testing four hypotheses about its geometric properties. The results are contrary to three of these hypotheses: that primary spatial knowledge is Euclidean, consists of topological neighborhoods, or preserves whatever geometric properties are constant during learning. Our findings support the hypothesis that primary spatial knowledge is best described as a place graph in which edges are labeled with local information about the approximate path lengths between places and intersections, and nodes are labeled with local information about objects and the approximate angles between paths.

Supplementary Material

The supplementary material for this article includes an additional comparison of experiments. The data supporting this article may be accessed from the Brown University Digital Repository https://repository.library.brown.edu/studio/item/bdr:1095248/

Acknowledgments

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Supplementary Material

Comparison of experiments

To integrate the findings of Experiments 1 and 2, we compare the results of the three tasks (metric shortcut, neighborhood shortcut, route) across the three environments (Control, Elastic, and Swap Mazes). To simplify the comparison, we analyze the absolute angular error in each condition. The mean absolute error (AE) was computed from the absolute value of the CE [0º, 180º] on each trial, and thus reflects both CE and VE. For each task, the predictions of the four main hypotheses (Euclidean, Neighborhood, Cognitive Graph, and Constancy hypotheses) and the experimental outcomes are summarized in Table 3.

1. Metric shortcut task

The metric shortcut task was primarily designed to investigate the Euclidean hypothesis by varying metric relations (Elastic Maze) or holding them invariant (Control Maze). If primary spatial knowledge is Euclidean, shortcuts should be less accurate or more variable in the Elastic Maze (because target locations were stretched 3m) than in the Control Maze. Contrary to this expectation, we found no significant differences in CE or VE between the Elastic Maze and the Control Maze (see Section 2.3.2). However, shortcuts were highly variable in both mazes, with mean within-subject VEs of 30.9˚-36.6˚. This is reflected in the large mean AEs (Figure 10A,B). Separate ANOVAs on angular errors in probe and control trials found no effects of environment ($p > .05$), and Bayes factors indicated anecdotal evidence for the null hypothesis ($BF_{01} = 2.58$ and 2.64 respectively).

These results are consistent with two possibilities: (1) spatial knowledge is Euclidean but highly imprecise, or (2) spatial knowledge is a non-Euclidean labelled graph. However, a noisy Euclidean map cannot explain the results of the neighborhood shortcut and route tasks.

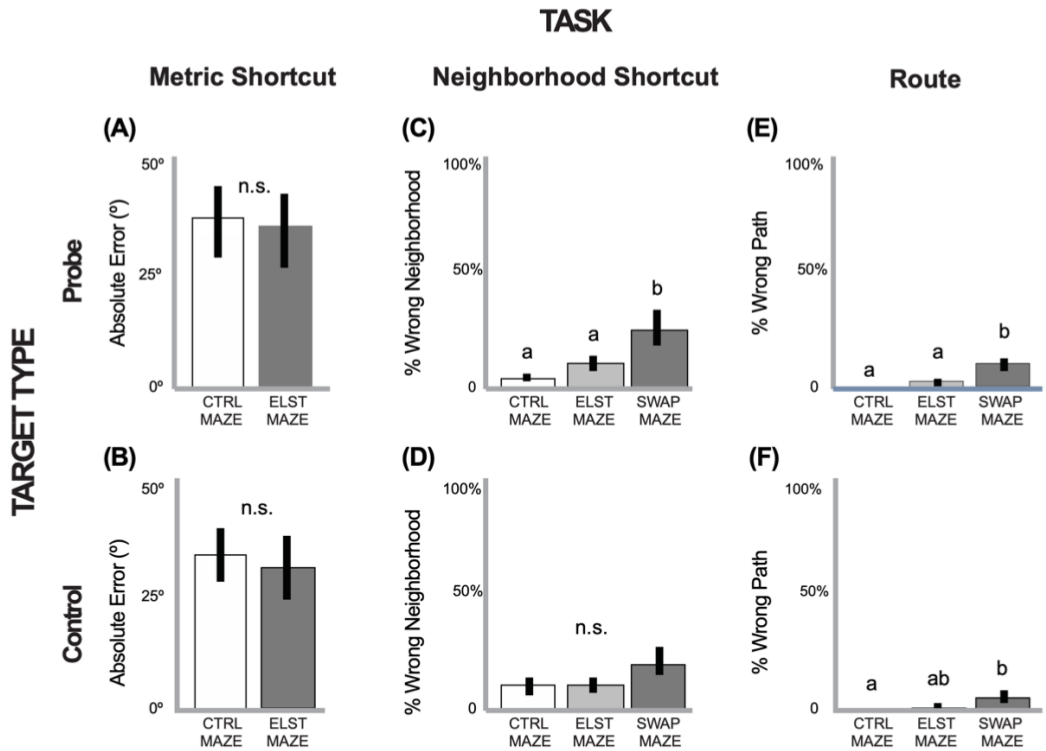

Figure 10. Comparison of experiments by task. *Left column (A, B)*: performance on the Metric Shortcut Task as measured by mean absolute angular error (AE). *Center column (C, D)*: performance on the Neighborhood Shortcut Task as measured by mean percentage of endpoints falling in wrong neighborhoods (defined as any non-short/long neighborhood in the Elastic Maze, and any non-A/B neighborhood in the Swap Maze). Endpoints falling on maze paths were excluded from percentage calculations. *Right column (E, F)*: performance on the Route Task as measured by the mean percentage of trials in which participants walked down an incorrect path. *Top row:* probe trials. *Bottom row*: control trials. Error bars indicate ±1 SEM. Duncan flags denote significant Tukey tests ($p < .05$); n.s. denotes non-significant one-way ANOVA.

2. Neighborhood shortcut task

The neighborhood shortcut task was designed to investigate the Neighborhood hypothesis by holding only neighborhoods constant (Swap Maze), only the place graph constant (Elastic Maze), or all geometric properties constant (Control Maze) during learning. The Neighborhood and Constancy Hypotheses predict that neighborhood shortcuts should be equivalent in the Swap and Control Mazes, for neighborhoods (defined by the Y-shaped skeleton) were invariant. On the other hand, if neighborhoods are derived from metric relations among places and boundaries, then performance should decline in the Elastic Maze, where those relations varied. Finally, if neighborhoods are derived from the place graph, then performance should decline in the Swap Maze, where node and edge assignments in the graph varied while the skeleton remained constant.

We found that neighborhood shortcuts were equivalent in the Elastic Maze and the Control Maze, indicating that neighborhoods are not derived from Euclidean structure (see Section 2.3.4). We also observed that VE was significantly larger in the Swap Maze than the Control Maze, despite constant neighborhoods (see Section 3.3.3), contrary to both the Neighborhood and Constancy hypotheses. Across experiments, we also find significantly more neighborhood shortcut errors on probe trials in the Swap Maze than the other mazes (Figure 10C,D): a one-way ANOVA on endpoints found a significant effect of environment, $F(2,33) = 3.30$, $p < .05$, $\eta_G^2 = .16$; post-hoc Tukey tests revealed that the wrong neighborhood was chosen more often in the Swap Maze (M = 25.9%, SD = 25.5%) than in the Control Maze (M = 6.9%, SD = 0.08%). No significant effects were found.

Thus, results for the neighborhood shortcut task contradict the Neighborhood and Constancy Hypotheses, but are consistent with the Cognitive Graph hypothesis. When the place graph was varied in the Swap Maze, shortcuts deteriorated, despite the fact that neighborhoods were constant. This strongly implies that neighborhoods are derived from the place graph.

3. Route Task

The route task was designed to investigate the Cognitive Graph hypothesis by holding only the place graph constant (Elastic Maze), only neighborhoods constant (Swap Maze), or all geometric properties constant (Control Maze) during learning. If graph knowledge is primary, then path choices should be unimodal (to A) in the Elastic and Control Mazes, but bimodal (to A and B) in the Swap Maze. On the other hand, if graph knowledge is derived from Euclidean structure, path choices should be bimodal in the Elastic Maze, because the stretched target falls in a different corridor. Finally, the Constancy hypothesis predicts that participants should choose the correct path (unimodal) in the Elastic Maze because the graph was constant, but take various paths to the correct neighborhood in the Swap Maze because only neighborhoods were constant.

Performance on the Route Task was overwhelmingly accurate in all three mazes (Figure 10E,F), with unimodal path choices in the Elastic and Control Mazes and bimodal choices in the Swap Maze. These results were consistent with the Graph hypothesis but not the Euclidean and Constancy hypotheses. Due to the variation in the graph of the Swap Maze, it was harder to learn in the training phase, and there were slightly more path errors in the test phase. For probe trials, an ANOVA on the percentage of wrong paths revealed a significant effect of environment, $F(2,32) = 6.88$, $p < .01$, $\eta_G^2 = .30$ ($BF_{10} = 12.9$, strong evidence for H_1); post-hoc Tukey tests revealed that wrong paths were chosen more often in the Swap Maze ($M = 9.8\%$, $SD = 10.5\%$) than in the Elastic ($M = 2.7\%$, $SD = 4.4\%$) or Control ($M = 0.24\%$, $SD = 0.82\%$) Mazes. For control trials, there was a significant effect of environment, $F(2,32) = 3.8$, $p < .05$, $\eta_G^2 = .19$ ($BF_{10} = 2.14$, anecdotal evidence for H_1), with more wrong paths chosen in the Swap Maze ($M = 5.13\%$, $SD = 6.96\%$) than in the Control Maze ($M = 0\%$, $SD = 0\%$); no other significant differences were found. Varying the place graph of the Swap Maze thus led to slightly more path errors. But despite this variation, participants chose correct routes on over 96% of trials, indicating that they successfully learned the graph of the Swap Maze. These results support the Cognitive Graph hypothesis that the primary form of spatial knowledge resembles a place graph.

4. Debriefing

An ANOVA on self-reported average number of hours spent playing video games revealed a significant effect of participant group, $F(7,89) = 2.33$, $p < .05$, $\eta_G^2 = .16$. A Tukey's HSD test revealed that participants in the Swap Maze / Neighborhood task group reported spending more time playing games that do not involve learning a spatial layout ($M = 4.03$ hr/week, $SD = 4.63$ hr/week) than in the Euclidean Maze / Route task group ($M = 0.80$, $SD = 1.09$ hr/week). However, the corresponding Bayes Factor was small ($BF_{10} = 1.6$) indicating only anecdotal evidence for the alternative hypothesis. Thus, differences in performance between groups are not attributable to video game experience.

An ANOVA on self-reported level of immersion in the virtual environment revealed a significant main effect of participant group, $F(7,89) = 2.69$, $p < .05$, $\eta_G^2 = .17$ ($BF_{10} = 3.26$, substantial evidence for H_1) . However, none of the pairwise Tukey tests reached significance (all *p*s > .05), while Bayes factors only supported a higher level of immersion in the Swap Maze/route task group than groups doing other tasks (Swap Maze/neighborhood shortcuts, $BF_{10} = 8.21$; Control Maze/neighborhood shortcuts, $BF_{10} = 4.86$; Control Maze/metric shortcuts, $BF_{10} = 7.93$). Overall, however, differences in performance between groups are not attributable to self-reported level of immersion.

Separate ANOVAs on individual items of the SBSOD failed to reach significance (all ps > .05, all $BF_{10} < 1$), indicating no evidence for any differences between participant groups. Across the 15 items, support for the null hypothesis ranged from anecdotal ($BF_{01} = 1.07$) to very strong ($BF_{01} = 33.6$). Thus, differences in performance between groups are not attributable to differences in self-rated spatial ability.

ANOVAs on the total number of responses and total number of correct responses for the RMT failed to reveal a significant effect of participant group (all ps > .05). The corresponding Bayesian analysis revealed strong evidence for the null hypothesis ($12.9 < BF_{01} < 17.4$). Thus, differences in performance between groups are not attributable to mental rotation ability.

ANOVAs on the CE and VE of responses to the PTSOT failed to reach significance (all *p*s > .05). The corresponding Bayesian analysis revealed decisive evidence (CE: $BF_{01} >> 100$) and substantial evidence (VE: $BF_{01} = 3.66$) for the null hypothesis respectively. Thus, differences in performance between groups are not attributable to perspective-taking ability.

The bidimensional regression analysis, which correlated the coordinates of objects in the sketch maps with their actual coordinates in the maze, failed to yield any inter-group differences in the main indices of translation, rotation, expansion, or general distortion (Tukey HSD > .05; $2.95 < BF_{01} < 11.7$, anecdotal to strong evidence for the null hypothesis). The one exception was a minor measure: the maximum value of unexplained variance was significantly greater for the route task group in the Elastic Maze than for the neighborhood shortcut group in the Elastic Maze ($p < .001$; $BF_{10} = 140.9$, decisive evidence for H_1) and the metric shortcut group in the Euclidean Maze ($p < .05$; $BF_{10} = 22.8$, strong evidence for H_1).

5. Conclusions

Taken together, the results of Experiments 1 and 2 are inconsistent with the Euclidean, Neighborhood and Constancy Hypotheses, but support the Cognitive Graph hypothesis (see Table 1, “Results” column). We expected that the primary geometry of spatial knowledge would be revealed by a specific pattern of results: performance on a given task should be high when the corresponding geometric property was constant during learning, but lower when that property was varied. (1) Euclidean structure does not fit this pattern, for metric shortcuts were always poor, and were unaffected when metric structure was varied (Elastic and Control Mazes). (2) Neither does Neighborhood structure, for neighborhood shortcuts declined when neighborhoods were held constant (Swap Maze); this result also contradicts the Constancy hypothesis. (3) Graph structure explains the data better than expected: performance on the route task is uniformly high across all mazes, both when the place graph was invariant (Elastic Maze) *and* when it was varied (Swap Maze). Learning and path choice decline slightly in the Swap Maze, as might be expected, but participants managed to learn bistable edge and node assignments and acquire a reliable place graph.

These findings lead us to conclude that primary spatial knowledge is best described as a labelled place graph, which incorporates local information about approximate path lengths and junction angles between known places. Neighborhood relations are derived from the place graph, based on information for neighborhood boundaries carried by edges and nodes.