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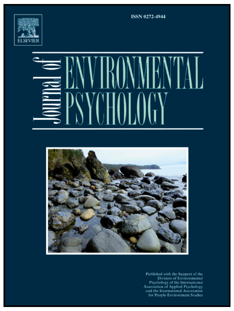

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# The role of distal landmarks and individual differences in acquiring spatial representations that support flexible and automatic wayfinding

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## Abstract

Theories of parallel memory systems suggest that flexible wayfinding (e.g., shortcutting) requires knowledge about the spatial structure of an environment, whereas automatic wayfinding (e.g., route-following) does not. Distal landmarks have widely been assumed to promote learning a spatial representation of an environment and, thus, flexible wayfinding through it. There is, however, little behavioural evidence to corroborate this assumption. In three experiments reported here, participants learned a circuitous route through a large-scale virtual garden maze, after which they completed orientation and wayfinding tests that measured their knowledge of the spatial structure of the environment and ability to shortcut through it, respectively. In Experiment 1, we found no evidence of a benefit to navigation in the presence versus the absence of distal landmarks when participants had continuous experience of the learned route, but pointing accuracy and shortcutting ability decreased when the learned route was complex compared to simple. In Experiment 2, participants learned a simple circuitous route in segments, and we observed superior knowledge of how the separately learned local spaces were aligned in the presence versus the absence of distal landmarks. Across all experiments, consistent with parallel memory systems, we observed that knowledge of the spatial structure of the environment was related

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to shortcutting but not route-following. This pattern of data suggests that distal landmarks promote the integration of separately learned local spaces into a coherent global representation, but do not promote learning of local spaces beyond what can be achieved by tracking self-motion.

**Keywords:** Distal landmarks; Individual differences; Cognitive map; Cognitive graph; Parallel memory systems; flexible (goal-directed) navigation

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## Abstract

Theories of parallel memory systems suggest that flexible wayfinding (e.g., shortcutting) requires knowledge about the spatial structure of an environment, whereas automatic wayfinding (e.g., route-following) does not. Distal landmarks have widely been assumed to promote learning a spatial representation of an environment and, thus, flexible wayfinding through it. There is, however, little behavioural evidence to corroborate this assumption. In three experiments reported here, participants learned a circuitous route through a large-scale virtual garden maze, after which they completed orientation and wayfinding tests that measured their knowledge of the spatial structure of the environment and ability to shortcut through it, respectively. In Experiment 1, we found no evidence of a benefit to navigation in the presence versus the absence of distal landmarks when participants had continuous experience of the learned route, but pointing accuracy and shortcutting ability decreased when the learned route was complex compared to simple. In Experiment 2, participants learned a simple circuitous route in segments, and we observed superior knowledge of how the separately learned local spaces were aligned in the presence versus the absence of distal landmarks. Across all experiments, consistent with parallel memory systems, we observed that knowledge of the spatial structure of the environment was related to shortcutting but not route-following. This pattern of data suggests that distal landmarks promote the integration of separately learned local spaces into a coherent global representation, but do not promote learning of local spaces beyond what can be achieved by tracking self-motion.

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## 1. Introduction

Wayfinding is a fundamental component of daily life. Commuting to-and-from work, buying goods from various shops, and sightseeing in new cities, all require the ability to get from one place to another and usually necessitate returning to a home location. These different wayfinding behaviours are supported by different types of spatial knowledge (e.g., Golledge, 1999; Montello, 1998; Siegel & White, 1975) – which can be learned at the same time (i.e., in parallel - Ishikawa & Montello, 2006). For instance, commuting between work and home can be achieved on the basis of route-knowledge, in which a navigator encodes the sequence of places and turns along a well-known route. In contrast, taking the shortest route home having visited multiple attractions requires knowledge about the spatial relations between places that have been visited. Broadly, the spatial structure of an environment can be learned in the form of allocentric survey-knowledge (e.g., Ishikawa & Montello, 2006), in which navigators encode the spatial relations among places in an environment, and egocentric self-to-object knowledge (e.g., Münzer et al., 2016), in which navigators acquire knowledge about the directional relations between their current location and orientation and environmental cues (e.g., landmarks).

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During wayfinding navigators must engage in planning and decision-making processes that require some form of spatial knowledge about the environment (Montello, 2001, 2005). There is consensus that human decision-making is controlled by parallel memory systems, with one system supporting flexible decision-making, and another system in which decisions are produced automatically (e.g., Balleine & Dickinson, 1998; Sutton & Barto, 2018). In navigation, different spatial representations originate from the different rules that govern learning in these separate memory systems. For instance, according to the proposals of cognitive mapping (and reinforcement learning) automatic navigation is controlled by a taxon (model-free) system in which navigators encode egocentric stimulus-

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response (landmark-action) associations. Here, a particular landmark or snapshot view evokes a turning response, such as left at the church, and by chaining a series of stimulus-response associations together navigators can traverse fixed routes through an environment (i.e., acquire route knowledge). Whilst automatic learning is cognitively efficient, it cannot guide navigational decision-making when, for instance, known routes are unexpectedly blocked. Under these circumstances, behaviour is thought to be controlled by a locale (model-based) system that encodes the spatial relations between landmarks and places, such that navigators can rely on their knowledge about the spatial structure of an environment to traverse novel routes to a target location. Under the proposals of cognitive mapping (e.g., O'Keefe and Nadel, 1978; White & McDonald, 2002), knowledge about the spatial structure of an environment is thought to be encoded in an allocentric reference frame (i.e., navigators acquire survey knowledge), and is translated to an egocentric reference frame when it is retrieved during wayfinding (e.g., Epstein & Vass, 2014; see also Byrne et al., 2007). In contrast, reinforcement learning is agnostic in terms of the information that comprises a model of an environment (e.g., Khamassi & Humphries, 2012; see also Buckley et al., 2024; Peer et al., 2021); thus, knowledge about the spatial structure of an environment might take the form of allocentric survey, or egocentric self-to-object, knowledge.

Recently, there has been growing interest in understanding how the properties of an environment support learning its spatial structure and, therefore, flexible wayfinding within it (e.g., Gregorians & Spiers, 2022; Peer et al., 2021, 2024; Yesiltepe et al., 2023). In the navigation literature, the presence of distal landmarks that orient an environment has consistently been proposed to support encoding the allocentric relations among places and cues (e.g., O'Keefe & Nadel, 1978; White & McDonald, 2002). Moreover, some theories suggest we encode the distances and directions between places in an environment by tracking self-motion (e.g., McNaughton et al., 1996; Poucet, 1993; see also Anastasiou et al., 2022;

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Wang, 2016; Warren 2019), and distal landmarks support this process as they provide directional cues that permit the navigator to update their global position and heading (e.g., Etienne & Jeffery, 2004; McNaughton et al., 1996, 2006). During wayfinding, it has also been suggested that distal landmarks support the execution of changes in direction to reach a target location, or plan the trajectory of a novel route (e.g., He et al., 2022; Redhead et al., 2022). In addition to supporting navigational processes within a local environment, distal landmarks have been proposed to help when navigators must integrate separately learned spatial representations into a coherent global representation. For instance, in the network of reference frames theory (Meilinger, 2008), local spaces are encoded as vistas, and an entire environment can be comprised of multiple vistas. Navigating between these vistas is achieved by computing perspective transformations (i.e., rotations and translations), and distal landmarks that are visible from both the current and target vista can help navigators infer these perspective transformations.

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There is, then, widespread agreement that distal landmarks should support learning the spatial structure of an environment and flexible navigation within it; however, many of these proposals remain untested. Peer et al. (2024) recently demonstrated that an open environment surrounded by distal landmarks supported better judgements of distance and direction compared to a closed environment comprising corridors not oriented by distal landmarks – but multiple differences between the environments make it difficult to interpret what properties supported better learning in the open- versus closed-maze. In empirical studies of wayfinding, having learned a meandering fixed route, humans have been observed to take shortcuts in virtual environments that were oriented by distal landmarks (e.g., Redhead et al., 2022) or mountains (Marchette et al., 2011), but similar behaviours have also been reported when distal landmarks were absent (e.g., Anggraini et al., 2018; Boone et al., 2019; He et al., 2022 Yu et al., 2021). These latter results suggest flexible wayfinding is possible in the absence of distal landmarks, but it remains to be determined if *more* accurate representations of the spatial structure of environments and, therefore, more shortcutting, are apparent in the presence versus the absence of distal landmarks.

The primary purpose of the experiments reported here, therefore, was to examine the conditions under which distal landmarks promote learning a spatial representation that supports flexible navigation. To achieve this, we combined into a single paradigm a pointing task that measures knowledge about the spatial structure of an environment (e.g., Weisberg et al., 2014) and assessments of shortcutting and route-following in a dual-solution task (e.g., Marchette et al., 2011). Across three experiments participants learned a fixed circuitous route through a virtual garden maze that contained intramaze objects at some junctions. Having learned the circuitous route, participants completed 1) wayfinding tests, in which they could choose to navigate between objects using the trained route or a novel shortcut, and 2) orientation tests, in which they were placed at one object within the maze and asked to point to a second, occluded, object. These tests, therefore, examine egocentric self-to-object knowledge, and in Experiments 1a and 1b we examined if the presence of distal landmarks facilitated performance on these measures after participants had continuous experience of traversing the fixed route. In Experiment 2, we trained each half of a circuitous route separately, to examine the proposal that distal landmarks support navigation when behaviour requires the integration of separately learned local spaces into a coherent global reference frame (Meilinger, 2008).

In addition to examining the circumstances in which distal landmarks support navigation, we also examined individual differences (see Newcombe et al., 2023). In previous studies, the ability to point accurately between buildings encountered along fixed routes in one task has correlated with the ability to traverse novel shortcuts in a separate task (Weisberg & Newcombe, 2016), and the same pattern of data has recently been reported

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when measures of pointing and shortcutting were taken within the same environment (He et al., 2023). In the context of studying individual differences in navigation, however, there have been potential design issues with shortcutting and pointing tasks in previous research. In terms of shortcutting, previous studies have not controlled for the length of novel shortcuts relative to well-known routes, which is problematic because participants might be more likely to attempt shortcuts when there is a significant payoff relative to following a well-known path (Krichmar & He, 2023; Lancia et al., 2023: see also Kool et al., 2016, 2017, 2018 for non-spatial demonstrations). In terms of pointing, previous research has required participants to translate knowledge acquired by navigating through a 3D environment onto an abstract 2D representation of space (He et al., 2023; see also Peer et al., 2024), which might be particularly difficult for participants with lower spatial ability. In the present experiments, therefore, we designed a novel environment in which we controlled the relative lengths of shortcuts versus the trained route across all wayfinding tests, and examined pointing ability by placing participants at one object in the environment and asking them to rotate their first-person view until they were facing directly towards an (occluded) target object.

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Studying individual differences on our task also allowed us to examine the key tenet of parallel memory systems. According to this theoretical framework, we should observe that participants who show less error in pointing judgements are more able to calculate novel shortcuts through the environment; however, given that route-following does not require knowledge about the spatial structure of the environment, there should be no relation between pointing accuracy and the ability to follow the trained route.

## 2. Experiment 1

In Experiment 1a, participants were trained to follow a circuitous route past various intramaze objects within a virtual garden maze until they could repeat it without making an error. In a series of wayfinding tests that followed this training, participants were placed at one intramaze object and asked to navigate to a target intramaze object. In half of these tests, participants could navigate a novel shorter route (Shortcut-Available trials). In the other half, novel routes were available, but the shortest novel route was an equivalent length to the trained route (No Shortcut-Available trials). In a series of orientation tests conducted with the same intramaze objects used in the wayfinding tests, participants were placed at one object and asked to point to the target object (which was occluded by the walls of the garden maze). Importantly, one group of participants completed the entire experiment in the presence of prominent distal landmarks that could all be viewed from any position within the environment (Distal Group), whereas a second group completed the entire experiment in the absence of these landmarks (No Distal Group). As noted in the introduction, the presence of distal landmarks is thought to promote learning the allocentric relations among places in an environment (e.g., O’Keefe & Nadel, 1978; White & McDonald, 2002). Consequently, during the orientation tests that measured participants’ knowledge of the spatial structure of the environment, we expected the Distal Group to demonstrate more accurate pointing compared to the No Distal group. Moreover, given flexible wayfinding is thought to rely on knowledge of the spatial structure of the environment, we also anticipated more shortcutting in the Distal compared to the No Distal Group on wayfinding tests.

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In Experiment 1b we repeated the same protocol, but participants were required to learn a more complicated route compared to Experiment 1a. Here, we increased the number of turns along the trained route, so participants experienced more changes in heading direction. Given that previous research, conducted in the absence of any landmarks, has demonstrated that increases in path complexity result in less learning about the spatial structure of environments (e.g., O'Neill, 1992), we expected less accurate pointing and less shortcutting when participants in the No Distal Group learned a complex (Experiment 1b) compared to simple (Experiment 1a) route. As noted in the introduction, though, distal landmarks afford global directional cues that permit navigators to track their position and heading within the environment (e.g., Etienne & Jeffery, 2004; McNaughton et al., 1996, 2006). For participants in the Distal Group, therefore, we anticipated that pointing accuracy or the ability to take novel shortcuts would not decline significantly following our manipulation to path complexity.

### 2.1. Participants

Power calculations performed using G*Power 3.1 revealed 40 participants were required in each group (Supplementary Section 1). As data were collected, we screened individual responses to ensure participant engagement. To do this, we administered a short multiple-choice test following the instruction screens (section 2.3.1) to ensure participants had read and understood the task instructions. If a participant failed this test more than five times, their data were rejected. Moreover, on tests of orientation (see section 2.3.3.2), any participant that submitted a response in under one second without turning in the environment was also rejected. Any rejected data were replaced by recruiting additional participants, with recruitment stopping as soon as we had collected a sample of 80 participants who all passed the screening tests.

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Experiments 1a and 1b both lasted approximately 60 minutes, and were given ethical approval at Aston and Durham Universities. Participants were pseudo-randomly allocated to a group, with the constraint that males and females were equally distributed between groups. In Experiment 1a, a total of 81 participants were recruited via Prolific (app.prolific.co), and the final sample comprised 80 participants (40 female) aged between 18-40 (*M* = 29.58, *SD* = 6.13). Participants were paid £9.00/hr for taking part. In Experiment 1b, 84 participants were recruited via the Psychology Research Participation Schemes at Aston and Durham

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Universities, with the final sample comprising 80 participants (60 female) aged between 18-24 (*M* = 19.33, *SD* = 1.13).

## 2.2. Materials

To design our MOWN (Measures of Orientation and Wayfinding in Navigation) Garden Maze we began with a grid environment, and plotted a to-be-learned route through the environment that would allow us to systematically block paths to create two different wayfinding trial types in which the relative lengths of novel and trained paths were controlled. On Shortcut-Available trials our environment afforded a novel route that was shorter (3-junctions) than the trained route (5-junctions), whereas for No Shortcut-Available trials the shortest novel routes were equivalent to the trained route (both 5-junctions – see Figure 1).

The environment was constructed and programmed in Unity (version 2019.4.0f1 for Windows). A grass-texture was applied to the floor, and tiled slab texture applied to the walls. Both the intramaze objects (Supplementary Section 2) and distal landmarks (Figure 1) were sourced from the Unity Asset Store (https://assetstore.unity.com). We deliberately chose asymmetrical objects to serve as intramaze objects to provide participants in the No Distal Group a cue for orientation at the beginning of all wayfinding and orientation tests. Intramaze objects were placed in the centre of the 8 Unity units (Uu) x 8Uu junctions within the garden maze, and no two adjacent junctions contained these objects. In Figure 1, letters A through O represent the locations of objects in the environment, but the objects were randomly assigned to junctions at the beginning of the experiment for each participant. The corridors of the maze were 16Uu in length and 2.0Uu high, and participants viewed the environment from a camera placed 1.8Uu above the floor, which travelled forwards and backwards at a speed of 8Uu per second, and rotated 100° per second. Importantly, therefore, the walls occluded any

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intramaze objects that were not in a participant’s line of sight, but left all distal landmarks visible from any part of the environment.

All experiments presented in this manuscript were administered online. Participants were directed to our own research platform (psytester.com) and required to give informed consent to participate. Following this, participants were forwarded to the experiment itself, which was presented as a WebGL application within the participant’s browser. At the conclusion of the experiment all data were saved onto Psytester’s secure servers.

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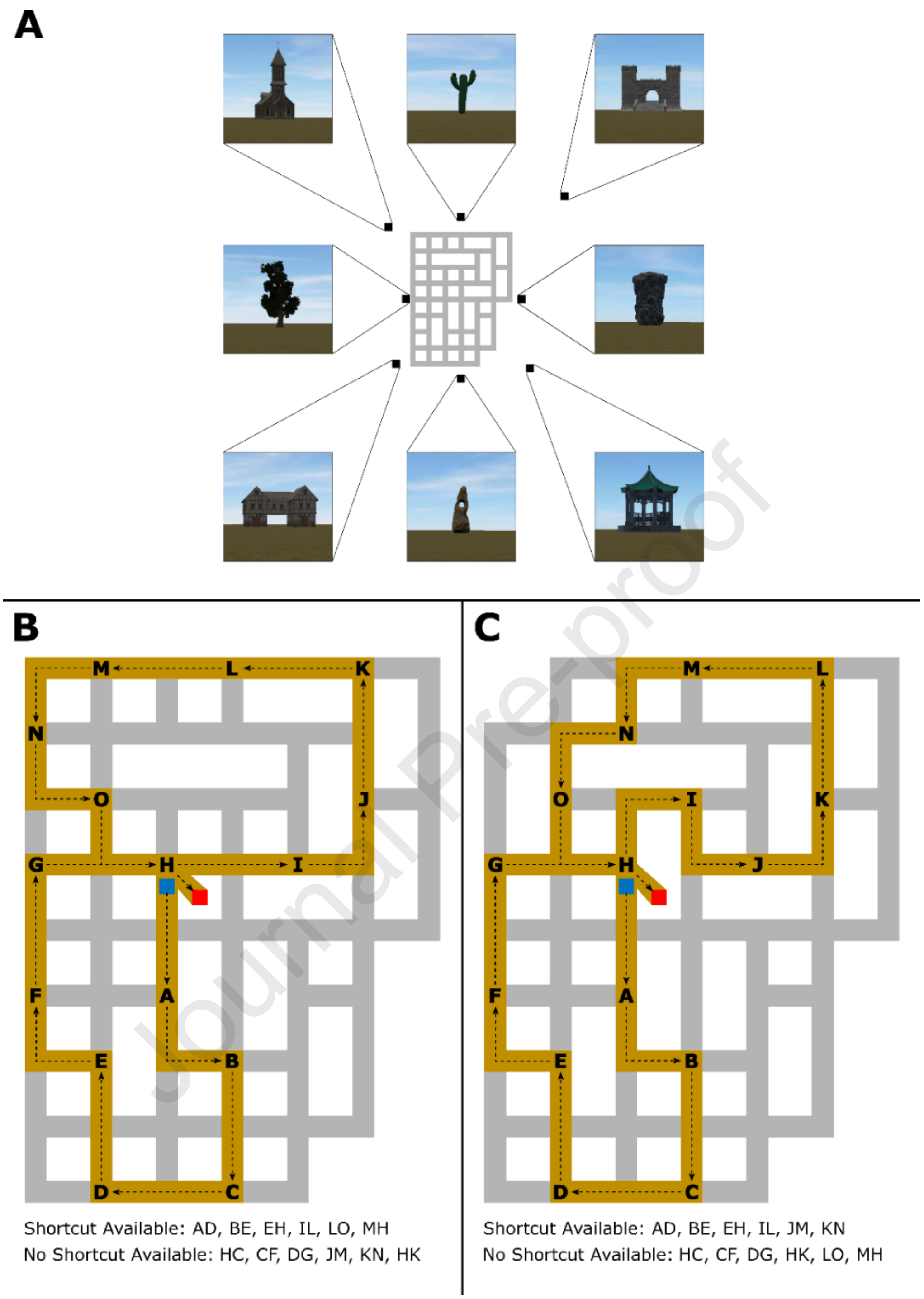

**Figure 1**. Schematic overviews of the MOWN garden maze environment. Panel A indicates the position of the distal landmarks, when present. The orange line in Panels B and C shows the simple and complex routes that participants were required to learn in Experiments 1a and 1b, respectively. The route began at the blue square, and ended once participants had entered the red square (which was only accessible once all fifteen landmarks had been visited). Letters denote the 15 junctions that contained an intramaze object, but objects were randomly assigned to these junctions for each participant. Following training, participants received 24 wayfinding (navigate to target) and orientation (point to target) tests. The object pairings that comprised these tests were split equally into two categories based on whether the environment afforded a novel shorter route (Shortcut-Available) or a novel route that was of equivalent length to the trained route (No Shortcut-Available) during wayfinding tests. The same object pairings were used during orientation tests.

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## 2.3. Procedure

### *2.3.1. Instructions*

Participants were told they would be required to learn a fixed route that they would view from a first-person perspective. Instructions were split across several screens (Supplementary Section 3.2), with a delay timer forcing participants to dwell on each screen for a length of time that was appropriate to read the text presented. To ensure participants had read and understood the instructions, they were required to correctly answer three yes-no questions before progressing to the training phase of the experiment (Supplementary Section 3.2.2). If an incorrect response was given to any question, participants were required to re-read the instructions and answer the questions again.

### *2.3.2 Training*

#### *2.3.2.1. Guided Learning*

We administered a series of trials designed to progressively shape learning of the route. Participants first watched a 170s video in which they were passively transported along the trained route. Participants then actively navigated through the garden maze using the cursor keys on the keyboard; here, pressing the up and down arrows moved the participant forwards and backwards, respectively, and presses on the right and left arrows permitted rotation in a clockwise and counterclockwise direction, respectively. In the first trial after the video, participants were guided around the route by blue arrows located on the floor at every junction (Figure 2). Participants were instructed that these arrows would be removed in later trials, so they should memorise the route they are following. On the next trial, the arrows appeared only as the participant approached a junction, and participants were instructed that they should attempt to predict the direction of travel at each junction before the arrows appeared. In all trials, if a participant traversed halfway along an incorrect arm, an invisible

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barrier prevented further travel and a message was displayed to inform participants to correct their path within 2Uu of this barrier.

*2.3.2.2. Training-to-Criterion.*

Participants were instructed that they would be required to walk the route unaided (i.e., there were no arrows to indicate correct choices at any junctions). Trials were administered until participants completed a single trial without making an error (i.e., without receiving a message to correct their path).

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*2.3.2.3. Partial Routes.*

Participants completed a block of six trials in which they were required to walk segments of the full route unaided (i.e., without arrows to indicate correct choices): Object H-to-L (quarter route, north section), object H-to-D (quarter route, south section), object L-to-H (quarter route, north section), object A-to-H (south half of full route), object D-to-H (quarter route, south section), object I-to-H (north half of full route). The order of these trials was pseudo-randomised such that the two half-route trials were not administered successively, and were administered in the same order for all participants.

The purpose of partial route trials was two-fold. First, these trials mimicked subsequent wayfinding tests in that they did not always begin at the start location, and so we reasoned that performance at test might be less affected by surprise compared to if there were no partial route trials administered. Second, as the training trials preceding the partial route trials always required traversing the full route, some participants may have encoded the route as a verbal sequence of turns (e.g., straight, left, right). By having trials that did not begin at the start of the route, we reasoned that we would discourage this verbal strategy as any participants navigating by reproducing a verbal list of turns would be lost when trials did not start from the beginning of that memorised list (Buckley et al., 2024: see also Grzeschik, 2019).

#### *2.3.2.4. Retraining-to-Criterion.*

We again administered trials in which participants were required to walk the full route unaided (i.e., without arrows), to ensure partial route trials had not disrupted performance prior to tests being administered. As before, these trials continued until a participant completed a single trial without making an error.

### *2.3.3. Tests*

#### *2.3.3.1. Wayfinding*

Participants were instructed that they would begin facing an object as if they were walking the trained route, and would be required to navigate to the second object along any path in the environment. On each trial, the start and target objects were displayed in the top left and right of the screen, respectively (see Figure 2). Shortcut-Available and No Shortcut-Available trials were presented in a block of 12 trials that was repeated twice for each participant. Within each block, the order of trials was pseudo-randomised such that no more than two of the same trial type were presented consecutively.

#### *2.3.3.2. Orientation*

Participants were placed at one object along the route, as if they were walking the trained route, and asked to rotate their view until they thought they were facing a second (occluded) object, before pressing the space bar to submit a response. As with wayfinding tests, on each trial the start and target objects were displayed in the top left and right of the screen, respectively. A crosshair was present on screen to indicate precisely to participants their current pointing direction. The object pairings that comprised orientation tests were the

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same as those used in the wayfinding tests, and presentation of object pairings was yoked to the order that wayfinding tests were presented for each participant. Importantly, the order of trials was determined prior to the experiment beginning, so we could counterbalance presentation of wayfinding and orientation tests across participants.

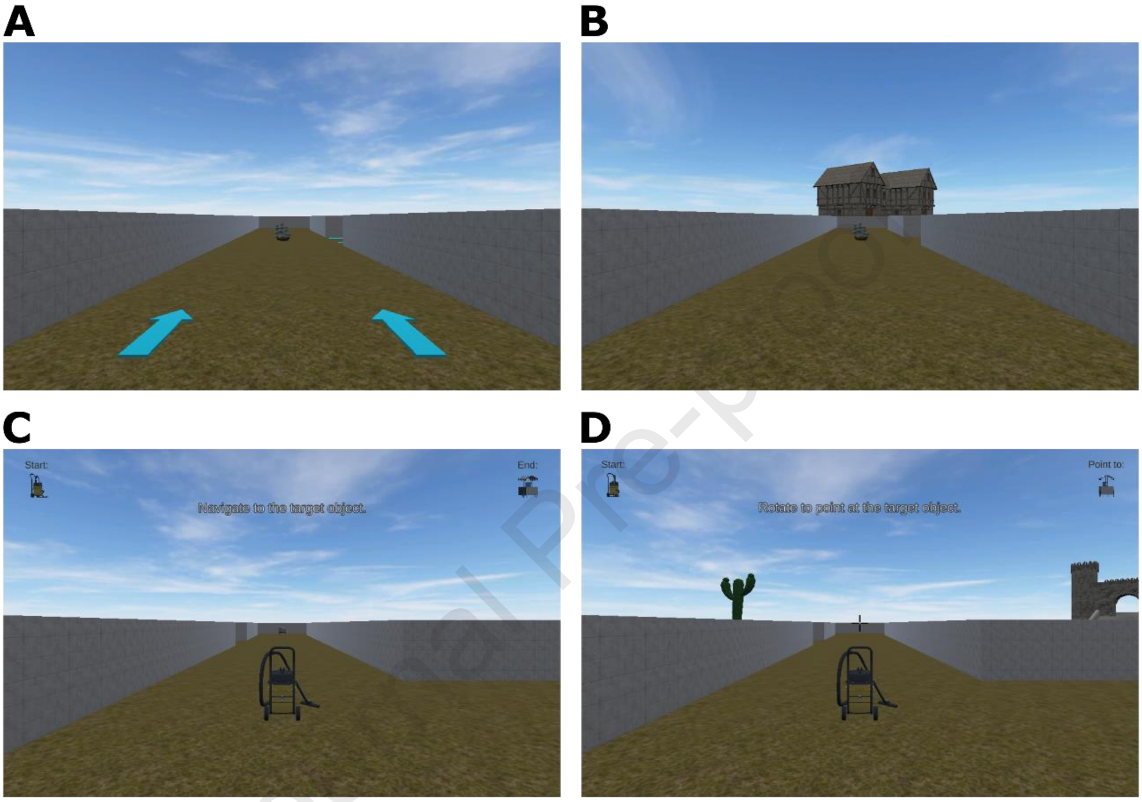

**Figure 2.** Screenshots of the appearance of the MOWN garden maze for the Distal (Panel B and D) and No Distal (Panel A and C) groups. Panel A, guided learning, in which arrows led the participant along the trained route. Panel B, training-to-criterion, in which participants were required to walk the entire route without making an error. Panel C, instructions at the beginning of a wayfinding test. Panel D, instructions at the beginning of an Orientation test, with a crosshair to denote the current pointing direction. For the duration of every test, the start and target objects were displayed in the top left and right of the screen, respectively. Videos of the appearance of our environment can be viewed in supplementary section 3.1.

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## 2.4. Measures

### *2.4.1. Training*

We recorded the number of trials required to complete the training- and retraining-to criterion phases of the experiment.

### *2.4.2. Orientation tests*

We recorded the absolute angular error between participant responses and correct responses for every trial (i.e., values were unsigned, and could range from 0-180).

### *2.4.3 Wayfinding tests*

During the Shortcut-Available trials, we coded whether participants followed the trained route, or took a novel route that was either shorter, of an equivalent length, or longer, than the trained route. The same data was coded for No Shortcut-Available trials, but novel routes shorter than the trained route were not possible. We note here that our measure of performance is different to previous examinations of wayfinding in which the distance participants travelled has been expressed as a function of the optimal path on each trial (e.g., Boone et al., 2018, 2019; He et al., 2023). We chose to do this because our discrete measure of junctions passed is less subject to variance arising from elements of the task that were not related to navigation (e.g., ability to control movement in a computer game).

## **2.5. Data Analysis**

All data reported in this manuscript and the supplementary materials are available at https://osf.io/e78yf/.

Statistical testing was performed with an alpha value of .05. To communicate effect sizes, we report Cohen's *d* for t-tests and *r* for correlations with 95% confidence intervals (CI). For analysis of variance (ANOVA), we report partial eta squared ($\eta_p^2$) and, in keeping with our previous work (e.g., Buckley et al., 2019a, 2021), we appropriately report 90% CIs (Steiger, 2004) to avoid paradoxically reporting significant *F*-tests that are accompanied by effect sizes with 95% CIs that include zero (see Lakens, 2013).

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### *2.5.1. Main manuscript*

In the results section below, we focus on reporting tests that directly address our hypotheses.

#### *2.5.1.1. Orientation tests*

We calculated a mean average pointing accuracy for each participant across all orientation tests. Performance of participants in the Distal and No Distal Groups, having learned a simple (Experiment 1a) or complex (Experiment 1b) route, was then compared. Performance of each group, in each experiment, was also compared to chance (90 degrees).

#### *2.5.1.2. Wayfinding tests*

For Shortcut-Available trials we calculated the proportion of each path taken by each participant. Given these proportions necessarily summed to 1 for every participant, we could not compare all wayfinding behaviour in a single analysis. As our primary interest concerned differences between flexible (shortcutting) and automatic (route-following) navigation, we compared these behaviours across Groups and Experiments.

#### *2.5.1.3. Individual Differences in Flexible and Automatic Navigation*

In keeping with other studies of individual differences in navigation (He et al., 2023; Weisberg et al., 2014; Weisberg & Newcombe, 2016), we performed cluster analysis based on K-means to determine if there were discrete categories of performance within our samples. Here, for each group in each experiment, we separately determined the optimal number of clusters within the data using the gap statistic method. In all but one analysis our data were best described by a single cluster (Supplementary Section 4). Consequently, to examine the relation between flexible and automatic navigational behaviour with knowledge about the spatial structure of the environment, we correlated: 1) the proportion of shortcuts on Shortcut-

Available Wayfinding tests with pointing accuracy between the same objects on Orientation tests, and 2) the proportion of paths that followed the trained route during No Shortcut-Available Wayfinding tests with pointing accuracy between the same objects.

In addition to the correlational analyses described above, we also report exploratory regressions to evaluate if the presence or absence of distal cues influenced the relationship between the measures taken from orientation wayfinding tests. Given that shortcutting behaviour is thought to require knowledge of the spatial structure of the environment, we examined if the proportion of shortcuts on Shortcut-Available Wayfinding tests could be predicted by pointing accuracy between the same objects on Orientation tests. We also performed the same analyses using measures taken from the No Shortcut-Available tests as the outcome and predictor. Crucially, we entered Group (Distal or No Distal) and the interaction between Group and pointing accuracy as additional predictors in all regression analyses.

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### *2.5.2. Supplementary materials*

#### *2.5.2.1. Training*

To verify participants learned our task, we compared the number of trials to reach criterion in the training- and retraining-to-criterion stages across Experiments and Groups (Supplementary Section 5).

#### *2.5.2.2. Wayfinding tests*

For No Shortcut-Available trials, we conducted an equivalent comparison to the analyses of Shortcut-Available trials, in which we compared the proportion of trials on which participants followed the trained route versus a novel route of equivalent length (Supplementary Section 7).

To provide context on wayfinding behaviour when participants did not take a novel shortcut or follow the trained route, we compared the proportion of trials on which participants became lost. As the chance of becoming lost may vary by wayfinding trial type (e.g., participants may be tempted to try novel routes on Shortcut-Available trials, but choose to follow the well-known route on No Shortcut-Available trials) we compare instances of lost navigation separately for the different trial types (Supplementary Sections 6 and 7).

## 3. Results

### 3.1. Orientation tests

One sample t-tests revealed that pointing error was significantly better than chance in both the Distal (Experiment 1a: $t(39) = 11.6$, $p < .001$, $d = 1.84$; Experiment 1b: $t(39) = 7.67$, $p < .001$, $d = 1.21$) and No Distal (Experiment 1a: $t(39) = 15.4$, $p < .001$, $d = 2.44$; Experiment 1b: $t(39) = 9.18$, $p < .001$, $d = 1.45$) Groups. Figure 3 shows that, whilst there was greater error in pointing on orientation tests in Experiment 1b compared to Experiment 1a, there appeared to be no differences between the Distal and No Distal groups in either experiment. A two-way ANOVA conducted on individual mean overall pointing errors, with between-subjects variables of Group (Distal or No Distal) and Experiment (1a or 1b), confirmed there was a significant main effect of Experiment $F(1,156) = 44.30$, $p < .001$, $\eta_p^2 = .22$ [.13, .31], but no main effect of Group $F(1,156) = .38$, $p = .54$, $\eta_p^2 = .002$ [.00, .03], and no interaction $F(1,156) = .60$, $p = .44$, $\eta_p^2 = .004$ [.00, .04].

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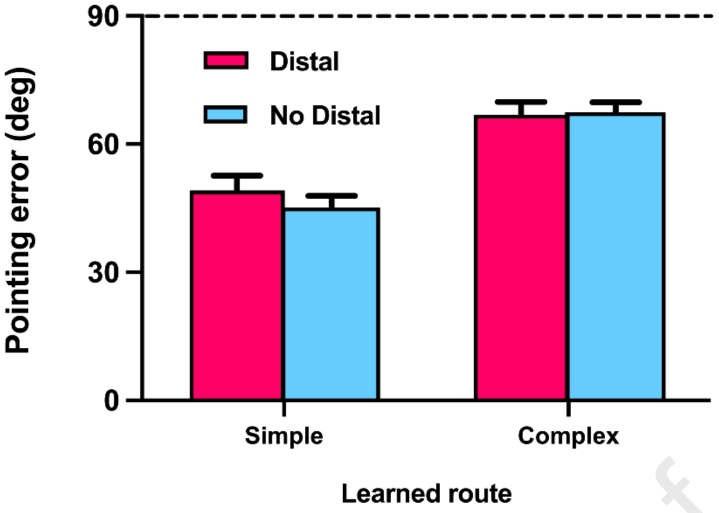

**Figure 3.** Overall pointing error on orientation tests for participants in the Distal and No Distal Groups having learned a simple (Experiment 1a) or complex (Experiment 1b) route. Error bars represent + 1 *SEM*, and the dotted line indicates chance performance.

### 3.2. Shortcut-Available Wayfinding Tests

Figure 4 shows that participants in Experiment 1a appeared to traverse novel shortcuts when they were available on wayfinding tests to a greater extent than they followed the trained route. In Experiment 1b, however, participants appeared to preferentially follow the trained route compared to traversing a novel shortcut. Again, in both experiments, there appeared to be no differences between the Distal and No Distal Groups.

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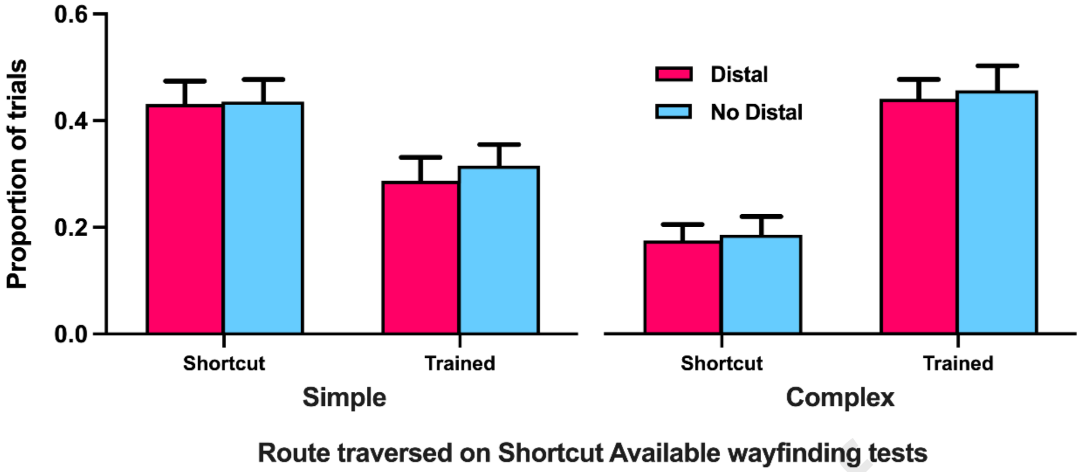

**Figure 4.** Proportion of trials on which participants took a novel shortcut or followed the trained route on Shortcut-Available wayfinding tests, having learned a simple (Experiment 1a) or complex (Experiment 1b) route. Error bars represent + 1 *SEM.*

A three-way ANOVA, with a within-subjects factor of Route Traversed (Shortcut or Trained), and between-subjects factors of Group (Distal or No Distal) and Experiment (1a or 1b) revealed no main effects of Group $F(1,156) = .94$, $p = .34$, $\eta_p^2 = .01$ [.00, .04], or Route Traversed $F(1,156) = 3.25$, $p = .07$, $\eta_p^2 = .02$ [.00, .07], but a significant main effect of Experiment $F(1,156) = 13.62$, $p < .001$, $\eta_p^2 = .08$ [.03, .15], and a significant interaction between Route Traversed and Experiment $F(1,156) = 28.70$, $p < .001$, $\eta_p^2 = .16$ [.08, .24]. Post-hoc simple main effects analysis revealed that, in Experiment 1, participants took the available shortcut more than they followed the trained route $t(156) = 2.51$, $p = .01$. In contrast, in Experiment 1b, participants followed the trained route more than they traversed a novel shortcut $t(156) = 5.06$, $p < .001$. The proportion of shortcuts was lower in Experiment 1b compared to Experiment 1a $t(156) = 6.71$, $p < .001$; and, complementing this finding, the proportion of trials in which participants followed the trained route was higher in Experiment 1b compared to Experiment 1a $t(156) = 3.46$, $p < .001$. The two-way interactions between Route and Group $F(1,156) = .03$, $p = .86$, $\eta_p^2 < .001$ [.00, .01], Group and Experiment $F(1,156)$

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= .01, $p$ =.92, $\eta_p^2$ <.001 [.00, .01], and the three-way interaction $F(1,156) = .02$, $p$ =.90, $\eta_p^2$ <.001 [.00, .01] were not significant.

## 3.3. Individual Differences in Flexible and Automatic Navigation

### *3.3.1. Shortcutting and Pointing Accuracy*

The left panels of Figure 5 show the correlation between the proportion of shortcuts taken on Shortcut-Available wayfinding tests and pointing error between the objects comprising the wayfinding tests. For both the Distal (Experiment 1a: $r(38) = -.62$ [-.78, -.38], $p < .001$; Experiment 1b: $r(38) = -.66$ [-.81, -.44], $p < .001$) and No Distal (Experiment 1a: $r(38) = -.58$ [-.75, -.33], $p$ <.001; Experiment 1b: $r(38) = -.46$ [-.66, -.18], $p$ =.003) Groups there was a strong negative correlation, such that smaller pointing error was related to more shortcutting. Regression analyses revealed that shortcutting on Shortcut-Available Wayfinding tests was predicted by pointing accuracy between the same objects during Orientation tests, but not Group or the interaction between Group and pointing accuracy (see table 1).

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### *3.3.2. Route-following and Pointing Accuracy*

The right panels of Figure 5 show the relation between proportion of trials on which the trained route was taken between two objects on No Shortcut-Available trials, and pointing error between the same objects. For both the Distal (Experiment 1a: $r(38) = .17$ [-.15, .46], $p$ = .30 ; Experiment 1b: $r(38) = .08$ [-.24, .38], $p$ = .63) and No Distal (Experiment 1a: $r(38) = .09$ [-.23, .39], $p$ = .58; Experiment 1b: $r(38) = .29$ [-.02, .55], $p$ = .07) Groups there was no relation between pointing error and proportion of trials in which the learned route was successfully followed. Regression analyses revealed that the proportion of trials on which participants followed the learned route on No Shortcut-Available Wayfinding tests was not predicted by pointing accuracy between the same objects during Orientation tests, Group, or the interaction term (see table 1)

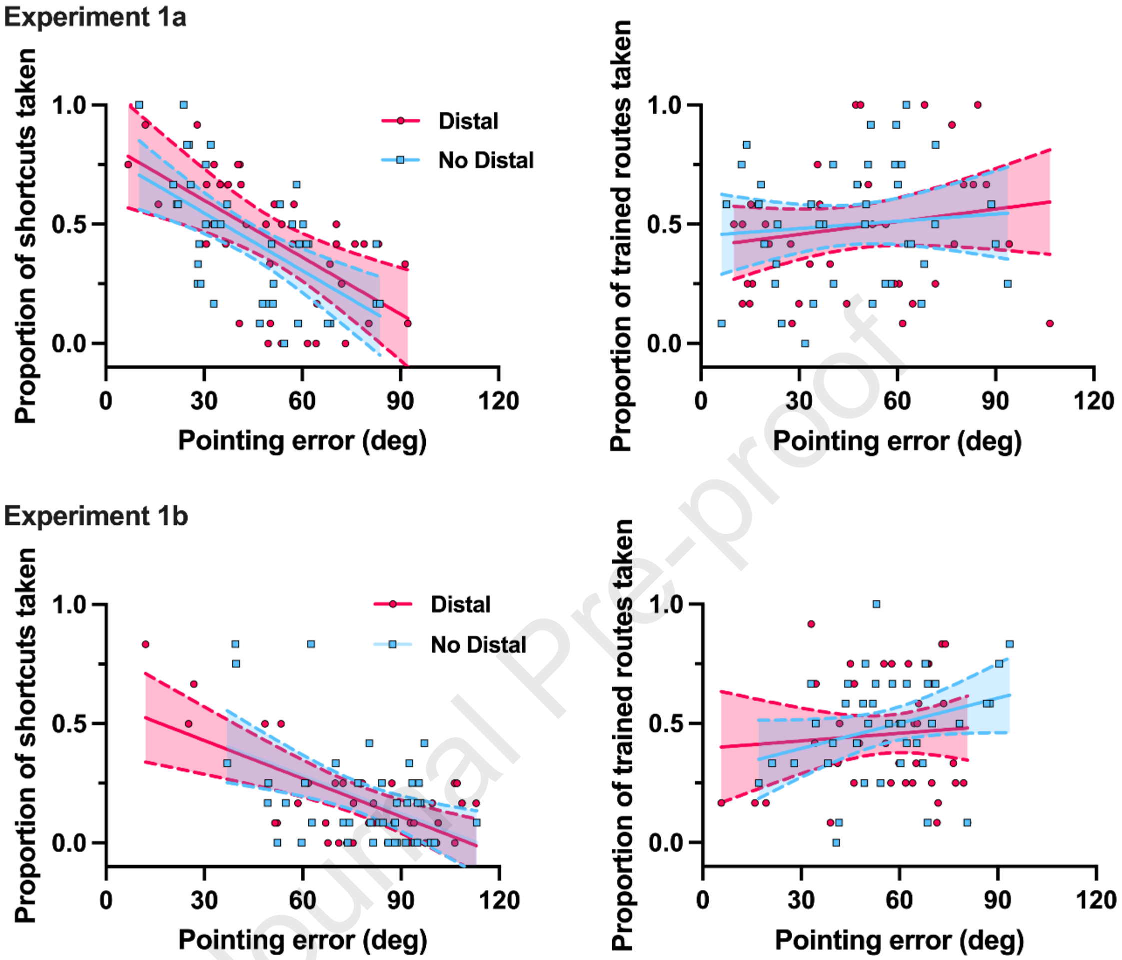

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**Figure 5.** Left Panels: Relation between the proportion of trials on which participants took a shortcut on Shortcut-Available trials and pointing error between the objects that comprised those Shortcut-Available trials having learned a simple (Experiment 1a) or complex (Experiment 1b) route. Right Panels: Relation between the proportion of trials on which participants followed the trained route on No Shortcut-Available trials and pointing error between the objects that comprised those No Shortcut-Available trials. Shaded regions represent the 95% CI.

Table 1: Regression model fits and coefficients from analyses in which shortcutting (proportion of shortcuts taken during Shortcut Available Wayfinding tests), and route-following (proportion of trials which followed the trained route during No Shortcut-Available Wayfinding tests), were entered as outcome variables, and pointing error between the objects that comprised the wayfinding tests, Group (Distal or No Distal), and the interaction between these variables were entered as predictors.

| | *B* (95% CI) | *SE B* | β | *p* |
|---|---|---|---|---|
| **Experiment 1a** | | | | |
| Shortcutting | | | | |
| Constant | .839 (.659 – 1.019) | .090 | | |
| Pointing Error | -.008 (-.011 - -.005) | .002 | -.608 | <.001 |
| Group | | | | |
| No Distal - Distal | -.051 (-.301 - .200) | .126 | -.205 | .206 |
| Pointing Error x Group | | | | |
| Pointing Error x (No Distal - Distal) | < -.001 (-.005 - .005) | .002 | -.007 | .971 |
| | $R^2$ = .361, *F*(3, 76) = 14.30, *p* < .001 | | | |
| Route following | | | | |
| Constant | .404 (.231 - .577) | .087 | | |
| Pointing Error | .002 (-.001 - .005) | .002 | .165 | .275 |
| Group | | | | |
| No Distal - Distal | .047 (-.211 - .305) | .130 | .044 | .720 |
| Pointing Error x Group | | | | |
| Pointing Error x (No Distal - Distal) | < -.001 (-.006 - .004) | .002 | .070 | .762 |
| | $R^2$ = .020, *F*(3, 76) = .511, *p* = .676 | | | |
| **Experiment 1b** | | | | |
| Shortcutting | | | | |
| Constant | .589 (.399 - .778) | .095 | | |
| Pointing Error | -.005 (-.008 - -.003) | .001 | -.557 | <.001 |
| Group | | | | |
| No Distal - Distal | .009 (-.290 - .309) | .150 | .063 | .950 |
| Pointing Error x Group | | | | |
| Pointing Error x (No Distal - Distal) | < .001 (-.004 - .004)) | .002 | .004 | .982 |
| | $R^2$ = .309, *F*(3, 76) = 11.30, *p* <.001 | | | |
| Route following | | | | |
| Constant | .395 (.159 - .630) | .118 | | |
| Pointing Error | .001 (-.003 - .005) | .002 | .083 | .599 |
| Group | | | | |
| No Distal - Distal | -.106 (-.441 - .230) | .169 | .138 | .533 |
| Pointing Error x Group | | | | |
| Pointing Error x (No Distal - Distal) | .002 (-.003 - .008) | .003 | .192 | .394 |
| | $R^2$ = .046, *F*(3, 76) = 1.23, *p* = .303 | | | |

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## 4. Discussion

In Experiments 1a and 1b participants learned a simple or complex fixed route, respectively, through a garden maze environment. After participants demonstrated they could walk the trained route without making an error, we administered wayfinding (navigate to target) and orientation (point to target) tests. Pointing performance in Experiment 1a was more accurate compared to Experiment 1b. Complementing this finding, during Shortcut-Available wayfinding tests, participants in Experiment 1a took novel shortcuts more than they followed the trained route, whereas the opposite pattern of performance was observed in Experiment 1b. Crucially, more shortcuts were taken in Experiment 1a compared to Experiment 1b, whereas participants followed the trained route more in Experiment 1b compared to Experiment 1a. Moreover, we also observed that participants became lost more often in Experiment 1b compared Experiment 1a (Supplementary Section 6). In summary, this pattern of data revealed that increasing the complexity of the trained route resulted in participants being less able to learn the spatial structure of the environment, a behavioural shift from flexible shortcutting towards route-following, and a propensity to become lost more often.

The effects that we observed in both orientation and wayfinding tests following our manipulation to path complexity suggest that participants in our task were relying on self-motion cues to learn the spatial structure of the environment. Whilst there was only a modest increase in the number of changes in direction along the trained routes of Experiment 1a and 1b, it is important to note that the effect of route complexity persisted despite the trained route between objects in Shortcut-Available trials being matched across experiments. That is, when travelling along the trained route between two objects that comprised Shortcut-Available trials in Experiment 1a and 1b, participants passed the same number of intramaze objects, and traversed the same number of arms and junctions in the environment. The effect

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of route complexity, therefore, cannot be attributed to uncontrolled factors such as relative differences in the length of the trained route versus available shortcuts. Moreover, we note that between Experiments 1a and 1b the learned route was only made more complex through the north section of the environment, with the route through the south section of the environment kept the same between experiments. Consistent with our conclusion that participants were relying on self-motion cues to learn the spatial structure of the environment, exploratory analyses revealed larger decreases in pointing accuracy between objects contained within the north compared to the south section of the environment following our path complexity manipulation (supplementary section 8.1.1).

One objection to our conclusion above is that the desktop virtual environment we used deprives participants of inputs that are considered important in tracking motion through real-world space, such as motor efference copy, proprioception, and vestibular information (see e.g., Poulter et al., 2018). It has, however, been demonstrated that optic flow is sufficient for human participants to maintain their sense of direction and location relative to environmental landmarks (Ellmore & McNaughton, 2004; see also Hilton & Wiener, 2023), and integrating time with the constant travel speed in our environment would also provide participants with information on distance travelled (Poulter et al., 2018).

A second objection to our conclusion is that tracking self-motion cues has been argued to be insufficient to guide navigation over long distances (e.g., Dudchenko, 2010; Eichenbaum & Cohen, 2014), because error accumulates as more distance and turns are traversed (e.g., Chapuis & Scardigli, 1993: see also Klatzky et al., 1990; Loomis et al., 1993; Rieser & Rider, 1991; Ruddle et al., 1998; Sholl, 1989). Recent theoretical perspectives, however, have argued that it is possible to learn the spatial structure of large scale environments on the basis of path integration. That is, providing self-motion cues can be used to encode the distance and direction from one place to the next (Anastasiou et al., 2022: see

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also Wang, 2016; Warren 2019), a representation of the entire environment can be formed as the navigator encodes multiple connections between adjacent places. We note that in our experiments participants may have used non-spatial mechanisms that are not usually considered part of path integration inputs to track self-motion, such as keeping track of turn directions in working memory. However, given that the pointing accuracy of participants in the No Distal Group was better than chance during orientation tests, our data are broadly consistent with the notion that large-scale environments can be learned on the basis of self-motion cues.

A third, and final, objection to our conclusion is that we did not observe that distal landmarks supported tracking self-motion, even when participants were required to learn the complex route of Experiment 1b. Distal landmarks, however, are not a pre-requisite for tracking self-motion (Etienne & Jeffery, 2004). It is, of course, difficult to draw theoretical conclusions based on null effects, but at the very least our findings suggest that the self-motion cues available to participants in the No Distal Group were sufficient for them to encode an accurate spatial representation of the environment, such that we could not detect any performance benefits to the presence of distal cues for the Distal Group. Nevertheless, given the widespread suggestion that distal landmarks promote learning the spatial structure of an environment (e.g., O'Keefe & Nadel, 1978; White & McDonald, 2002), support the tracking of self-motion (e.g., McNaughton et al., 1996: see also Peer et al., 2021), and help execute novel routes during wayfinding (e.g., He et al., 2022; Redhead et al., 2022), we were surprised to observe that the presence of distal landmarks did not help participants learn a continuously experienced environment, especially given that our measures of orientation and wayfinding examined egocentric self-to-object knowledge about the directional relations between the self and target locations (Münzer et al., 2016). In Experiment 2, we examined if

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distal landmarks support integrating separately learned local spaces into a coherent global representation.

## 5. Experiment 2

When participants learn segments of an environment separately, there are theoretically opposing viewpoints as to whether navigators combine separate representations of local spaces into a coherent global representation. For instance, Warren et al. (2017) reported that participants were able to calculate shortcuts between places in a virtual environment that violated the principles of Euclidean geometry and, moreover, that participants were unaware of the non-Euclidean nature of their environment. Based on these results, the authors argued that representations of local places were not embedded in a globally consistent reference frame. This proposal, however, contrasts with theories that suggest that local spatial representations are integrated. For instance, Mallot and Basten (2009) describe space-graphs, in which local places are encoded in a cognitive graph, and connected by embodied action rules (e.g., turn left 90 degrees, walk 2km). Locally encoded regions are themselves connected, such that they become the nodes of a higher order representation in a hierarchical graph. Consequently, locally encoded regions are necessarily embedded within a globally consistent reference frame (see also Poucet, 1993).

Since Experiment 1a and 1b failed to reveal any benefit of navigating in the presence of distal landmarks when a single route was learned continuously, in the present experiment we examined the theoretical proposal that distal landmarks promote embedding separately encoded local spaces into a common reference frame. Under the proposals of the network of reference frames theory (Meilinger, 2008), local spaces are encoded as separate vistas, and edges connecting these vistas denote the change in perspective required to move between them. The entire environment, comprised of multiple vistas, need not be encoded in a

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consistent reference frame; however, shortcuts are computed by imagining the perspective transformations required to reach a target location, and this requires spatial information to be brought into a common reference frame. According to Meilinger (2008), people can infer the perspective transformation between locally encoded spaces from any combination of 1) the immediate visual scene, 2) experience of navigating between two spaces, or 3) landmarks that are visible from both vistas.

Given the relative lack of shortcutting observed in Experiment 1b, participants in Experiment 2 learned the simple circuitous route used in Experiment 1a. In contrast to Experiment 1a, however, we trained participants to navigate through the diagrammatical north and south loops of the environment on separate trials. In addition to running the same tests that were administered in Experiment 1a, this permitted us to administer Cross-route tests, in which participants were asked to point and navigate between intramaze objects taken from separately learned local spaces. As with Experiments 1a and 1b, participants in the Distal and No Distal Group completed the experiment either in the presence or the absence of distal landmarks, respectively. Crucially, our training protocol ensured that participants did not directly experience navigating between the two halves of the environment, and during pointing tests the target intramaze object was occluded (i.e., not in the immediate visual scene). Consequently, according to the network of reference frames theory (Meilinger, 2008), only the Distal Group had access to cues that signalled how the separately trained routes were connected in global space. Under these circumstances, therefore, when participants were asked to navigate and point between objects contained on separately trained routes, we may expect better performance in the Distal Group compared to the No Distal Group. In contrast, if participants do not embed separately learned segments of an environment into a coherent reference frame (Warren et al., 2017), the presence of distal landmarks may do little to improve navigational performance in the Distal Group compared to the No Distal Group.

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Finally, in Experiment 2, we also wished to rule out the possibility that the lack of any differences between the Distal and No Distal groups in Experiment 1a and 1b was because participants in the Distal Group were not attending to the distal landmarks. If that were to be the case, then the distal landmarks would be rendered functionally absent in our design. To rule out this interpretation, in the present experiment participants in Group Distal Removed were trained in the presence of distal landmarks, which were then removed for the wayfinding and orientation tests. Based on similar designs conducted in our laboratory (e.g., Buckley et al., 2019b, 2021), we expected this manipulation to disrupt performance.

### *5.1. Participants*

Data exclusion followed the same criterion as previous experiments, and we again recruited 40 participants to each group. A total of 125 participants were recruited via Prolific (app.prolific.co), with the final sample comprising 120 participants (60 female) aged between 18-40 ($M = 29.12$, $SD = 5.64$). The study lasted approximately 90-minutes, and participants were paid £9.00/hr for taking part. Participants were pseudo-randomly allocated to a group, with the constraint that males and females were equally distributed between groups of the experiment, and between the counterbalanced conditions within a group (see procedure).

### *5.2. Materials*

In Experiment 1a, the intramaze object pairs used at test were located in either the diagrammatical north or south loop of the route, and so in the present experiment these objects comprised Within-route Shortcut-Available or Within-route No Shortcut-Available trials. In addition, we also administered Cross-route Shortcut-Available trials, in which object pairings comprised one object from each separately trained route segment (see Figure 6). On all Cross-route trials the shortest available path was 5-junctions, but trained routes varied from 8-21 junctions across trials.

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For participants in the No Distal group, the separately trained north and south loops ended by traversing the same corridor of the maze, in the same direction, to the same intramaze location. Consequently, it was possible for the No Distal group participants to infer that the two routes they learned were connected in an overall space. This information was also available to participants in the Distal Group, but distal landmarks visible from all regions of the environment provided additional information about how the separately trained routes were aligned.

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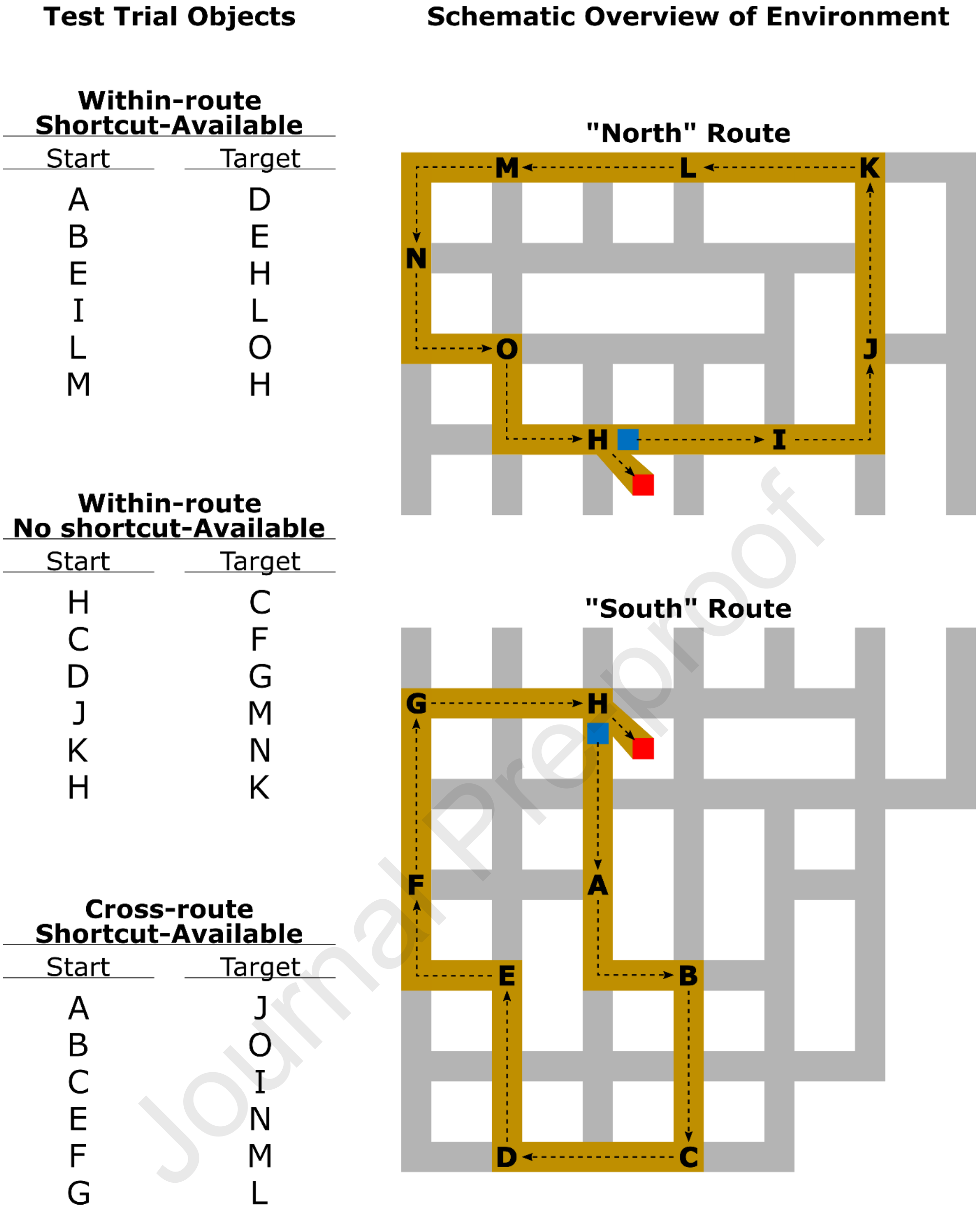

**Test Trial Objects**

**Within-route Shortcut-Available**

| Start | Target |
|---|---|
| A | D |
| B | E |
| E | H |
| I | L |
| L | O |
| M | H |

**Within-route No shortcut-Available**

| Start | Target |
|---|---|
| H | C |
| C | F |
| D | G |
| J | M |
| K | N |
| H | K |

**Cross-route Shortcut-Available**

| Start | Target |
|---|---|
| A | J |
| B | O |
| C | I |
| E | N |
| F | M |
| G | L |

**Figure 6.** Schematic diagram of the virtual environment used in Experiment 2, in which the diagrammatically North and South halves of the route used in Experiment 1a were trained separately. When learning each route, participants began at the blue square and ended at the red square. As participants navigated, they passed various objects positioned at the locations marked by letters. Following training, participants were asked to walk or point between objects. These trials were split into three categories based on whether the objects were contained in the same route, and whether or not a shortcut was available.

### *5.3. Procedure*

The training protocol and instructions (Supplementary Section 3.3) for all groups was broadly similar to Experiment 1a, save for the fact that participants learned the diagrammatically north (or south) loop followed by the south (or north) loop separately

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(counterbalanced across participants within each group). Here, participants progressed through the guided learning and training-to-criterion training phases for one route segment, before completing the same training phases for the other segment. Following this, participants completed partial route training and retraining-to-criterion for the first route segment they learned, before completing partial route trials and retraining-to-criterion for the second route segment. Partial route trials were formed from the same objects that comprised the partial route trials in Experiment 1a and, also in keeping with Experiment 1a, the order in which partial route trials were administered for the north (objects I-to-H, H-to-L, and L-to-H) and south (object A-to-H, H-to-D, and D-to-H) routes was the same for all participants.

Following training, participants again received wayfinding and orientation tests. The order in which these tests were administered was counterbalanced across the training order within each experimental group – such that the Distal, No Distal, and Distal Removed groups all had equal numbers of participants that learned the north or south loop first, and within the participants that learned the north (or south) loop first there were equal numbers of participants that completed the wayfinding or orientation tests first. Wayfinding tests were administered in 2 blocks of 18 trials, in which the six intramaze object pairs that formed the Within-route Shortcut-Available, Within-route No Shortcut-Available, and Cross-route Shortcut-Available trials were presented. The 18 trials that comprised a single block were further divided into 6 sub-blocks that contained one of each of the three trial types. As with Experiment 1a, the order of orientation tests was yoked to the order in which the participant experienced the wayfinding tests.

### *5.4. Measures*

Measures for the orientation tests, and within-route Shortcut-Available and No Shortcut-Available tests were the same as reported in Experiment 1a.

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#### *5.4.1. Cross-route wayfinding*

It was necessary to devise alternative dependent variables for the Cross-route wayfinding tests because the payoff for attempting a shortcut was so great relative to following the trained route. That is, because of the length of the trained route on some of these trials, we expected all participants to successfully complete some Cross-route shortcuts. We therefore examined the efficiency of Cross-route shortcuts by calculating for each participant: 1) the average lengths of shortcuts taken, and 2) the proportion of Cross-route trials in which participants perfectly executed a shortcut (i.e., traversed 5-junctions exactly).

### *5.5. Data Analysis*

#### *5.5.1. Main manuscript*

In the results section below we report the outcomes relating to Cross-route trials that address our hypothesis that distal landmarks support the integration of separately learned local spaces. Here, we examined between-group differences in pointing ability on objects that comprised the Cross-route Orientation tests using a one-way ANOVA. For wayfinding tests, we report equivalent comparisons to Experiment 1a, before comparing average lengths of shortcuts and proportions of perfectly executed shortcuts between groups using a one-way ANOVA. We again examined individual differences via correlations, and also in regression analyses in which measures from the wayfinding tests were used as outcomes to be predicted by pointing accuracy on Cross-route trials, Group, and the interaction between these variables.

#### *5.5.2. Supplementary materials*

Measures and analyses for objects that comprised the Within-route wayfinding and orientation tests were identical to those reported in Experiment 1a, and reported in

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supplementary materials (Section 11), alongside analyses of training data (Section 9), and lost navigation during Cross-route wayfinding tests (Section 10).

## 6. Results

### *6.1. Cross Route Orientation tests*

Pointing accuracy on Cross-route trials was better than chance in the Distal $t(39) = 7.91$, $p < .001$, $d = 1.25$, No Distal $t(39) = 5.29$, $p < .001$, $d = .84$, and Distal Removed $t(39) = 5.49$, $p < .001$, $d = .87$ Groups. The right panel of Figure 7 shows that pointing performance in the Distal Group appeared more accurate than the No Distal Group, and performance in the Distal Removed Group appeared disrupted relative to the Distal Group. A one-way ANOVA conducted with a between-subjects variable of Group (Distal, No Distal, or Distal Removed) revealed a significant omnibus effect, $F(2,117) = 3.99$, $p =. 02$, $\eta_p^2 = .06$ [.01, .14]. Post-hoc tests revealed better pointing accuracy in the Distal compared to the No Distal $t(117) = 2.24$, $p = .027$ and Distal Removed $t(117) = 2.61$, $p = .01$ Groups, but there was no significant difference between No Distal and Distal Removed Groups $t(117) = .37$, $p = .72$.

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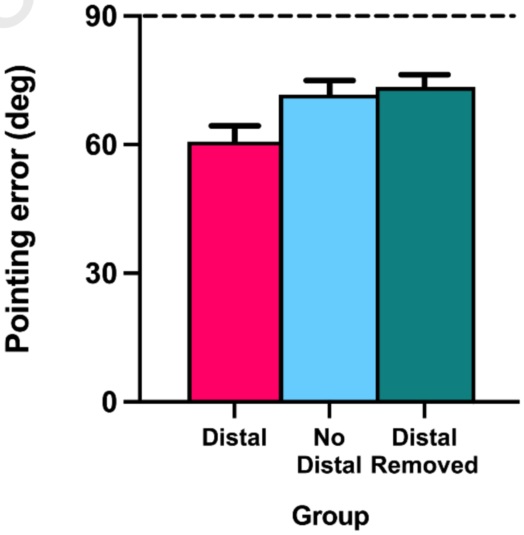

**Figure 7.** Pointing error on orientation tests that comprised the objects used for Cross-route Shortcut-Available Wayfinding tests for participants in the Distal, No Distal, and Distal Removed Groups of Experiment 2. Error bars represent + 1 *SEM*, and the dotted line indicates chance performance.

### *6.2. Cross-route Wayfinding tests*

As expected, there was a strong preference for taking a shortcut on Cross-route trials relative to following the trained route in all groups (Figure 8). A two-way ANOVA conducted on individual mean proportions of different routes taken, with a between-subjects variable of Group (Distal, No Distal, or Distal Removed), and a within-subjects variable of Route Traversed (Shortcut or Trained), revealed a significant main effect of Route Traversed $F(1, 117) = 1167.95$, $p < .001$, $\eta_p^2 = .91$ [.88, .92], but no effect of Group $F(2, 117) = .10$, $p = .90$, $\eta_p^2 = .002$ [.00, .01], and no interaction $F(2, 117) = 1.45$, $p = .24$, $\eta_p^2 = .02$ [.00, .08].

As planned, therefore, we examined navigational accuracy on Cross-route trials, and Figure 8 suggests that the number of junctions passed when taking a Cross-route shortcut was similar across all groups. A one-way ANOVA conducted on individual mean junctions passed when taking a Cross-route shortcut, with a between-subjects variable of Group (Distal, No Distal, or Distal Removed) revealed no significant differences between groups $F(2, 117) = .30$, $p = .74$, $\eta_p^2 = .01$ [.00, .03].

Figure 8 also suggests that the number of perfect shortcuts executed was similar across all groups. A one-way ANOVA conducted on individual mean proportions of perfect Cross-route shortcuts, with a between-subjects variable of Group (Distal, No Distal, or Distal Removed) revealed no significant differences between groups $F(2, 117) = 1.01$, $p = .37$, $\eta_p^2 = .02$ [.00, .06].

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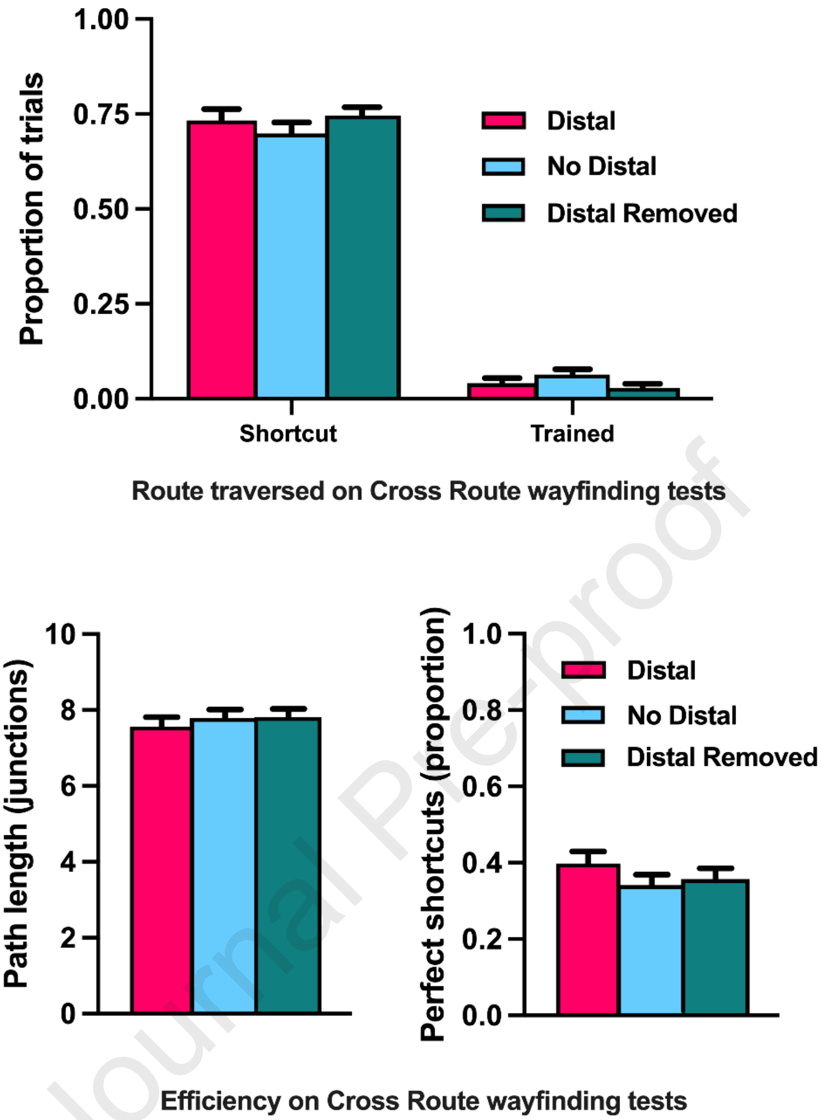

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**Figure 8.** Top panel, the proportion of trials on which participants took a novel shortcut or followed the trained route on Cross-route wayfinding tests. The bottom left panel shows the number of junctions passed by participants when taking a novel Cross-route shortcut, and the bottom right panel the proportion of trials on which participants navigated through exactly 5 junctions (the minimum possible) when taking a Cross-route shortcut. Error bars represent + 1*SEM*.

### *6.3. Individual Differences in flexible and automatic navigation*

Given the ceiling effect we observed with the high proportion of shortcuts taken on Cross-route trials, we examined the correlation between pointing performance and average number of junctions crossed. The left panel of Figure 9 shows the significant positive correlation between these variables in the Distal, *r*(38) = .34 [.04, .59], *p* = .03, No Distal, *r*(38) = .43 [.14, .66], *p* = .005, and Distal Removed, *r*(38) = .39 [.09, .63], *p* = .01, Groups, indicating that lower pointing error was associated with fewer junctions crossed. Regression analyses revealed that the average number of junctions crossed when a shortcut was taken on Cross-route trials was predicted by pointing accuracy between the same objects during Orientation tests, but not Group or the interaction between Group and pointing accuracy (see table 2).

We also examined the correlation between pointing accuracy and proportion of perfect shortcuts, which revealed a consistent pattern of data. The right panel of Figure 9 shows the significant negative relation between these variables in the Distal, *r*(38) = -.32 [-.58, -.01], *p* = .042, No Distal, *r*(38) = -.45 [-.67, -.16], *p* = .004, and Distal Removed, *r*(38) = -.42 [-.64, -,12], *p* = .008, Groups, indicating that lower pointing error was associated with more perfectly executed shortcuts. Regression analyses revealed that the proportion of perfect shortcuts was predicted by pointing accuracy, but not Group or the interaction between Group and pointing accuracy (see table 2).

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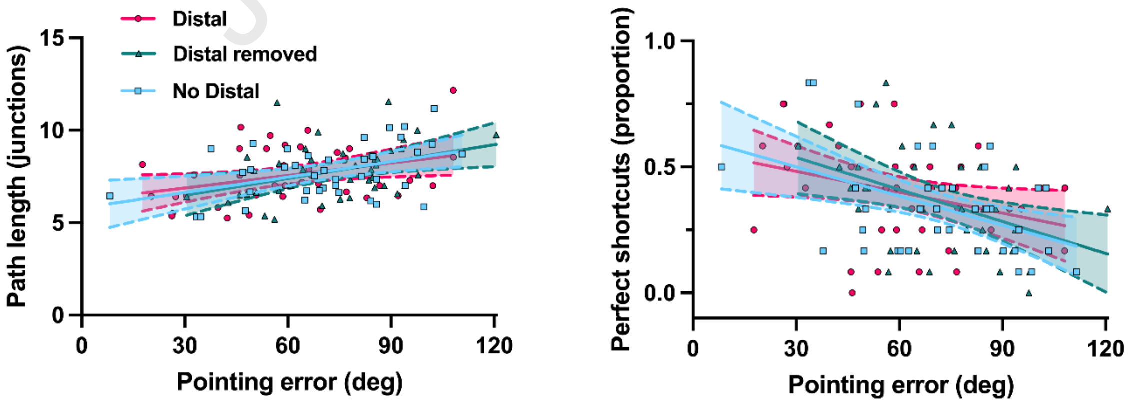

**Figure 9.** Left Panel: Relation between the average number of junctions passed when participants completed a shortcut and pointing error on Cross-route Shortcut-Available trials. Right Panel: Relation between the proportion of trials on which participants executed a perfect shortcut and pointing error on Cross-route Shortcut-Available trials. Shaded regions represent the 95% CI.

Table 2: Regression model fits and coefficients from analyses in which Cross-route shortcutting performance (average number of junctions crossed and proportion of perfectly executed shortcuts) was entered as the outcome variable, and pointing error between objects that comprised the cross-route wayfinding tests, Group (Distal, No Distal, and Distal Removed), and the interaction between these variables entered as predictors.

| | *B* (95% CI) | *SE B* | β | *p* |
|---|---|---|---|---|
| Junctions Crossed | | | | |
| Constant | 6.205 (4.990 – 7.420) | .613 | | |
| Pointing Error | .022 (.003 - .041) | .009 | .338 | .019 |
| Group | | | | |
| No Distal - Distal | -.413 (-2.333 – 1.507) | .969 | -.029 | .671 |
| Distal Removed - Distal | -.639 (-2.750 – 1.472) | 1.066 | -.064 | .550 |
| Pointing Error x Group | | | | |
| Pointing Error x (No Distal - Distal) | -.005 (-.022 - .033) | .014 | .082 | .695 |
| Pointing Error x (Distal Removed - Distal) | -.008 (-.022 - .038) | .015 | .120 | .595 |
| | $R^2 = .156$, $F(5, 114) = 4.20$, $p = .002$ | | | |
| Proportion of Perfect Shortcuts | | | | |
| Constant | .565 (.405 - .725) | .081 | | |
| Pointing Error | -.003 (-.005 - < -.001) | .001 | -.312 | .029 |
| Group | | | | |
| No Distal - Distal | .051 (-.202 - .304) | .128 | -.137 | .690 |
| Distal Removed - Distal | .099 (-.179 - .377) | .140 | -.009 | .483 |
| Pointing Error x Group | | | | |
| Pointing Error x (No Distal - Distal) | -.001 (-.005 - .002) | .002 | -.129 | .532 |
| Pointing Error x (Distal Removed - Distal) | -.001 (-.005 - .002) | .002 | -.166 | .456 |
| | $R^2 = .172$, $F(5, 114) = 4.74$, $p < .001$ | | | |

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## 7. Discussion

The present experiment contrasted opposing theoretical proposals about whether, or not, navigators embed locally encoded spaces into a coherent global reference. Having separately learned two fixed circuitous routes that were connected in global space, participants were given tests in which they were asked to navigate between, or point towards, intramaze objects they had encountered on the separately trained routes. Our analysis of Cross-route pointing performance revealed that participants in the Distal Group were significantly more accurate compared to the No Distal and Distal Removed Groups. Surprisingly, despite these differences in pointing performance, we observed no between group differences in the number of junctions traversed during Cross-route wayfinding tests, and there were also no differences in the proportion of perfectly executed shortcuts between groups. In keeping with Experiments 1a and 1b, there were no differences between the Distal and No Distal Groups on wayfinding tests conducted with objects within the same route (Supplementary Section 11.1.2), or on orientation tests when participants were asked to point between objects that comprised the wayfinding trials (Supplementary Section 11.1.1).

The pointing data from Experiment 2 provide evidence that locally encoded spaces are embedded into some form of global representation of space, as pointing accuracy in all groups was better than chance. Moreover, our observation that distal landmarks supported better pointing accuracy on Cross-route trials, relative to their absence in the No Distal and Distal Removed Groups, is consistent with the notion that landmarks that are visible from two separately encoded vista spaces support navigators in integrating separately learned local spaces (Meilinger, 2008). However, given that representations of the spatial structure of the environment are assumed to support flexible wayfinding behaviour (e.g., Khamassi & Humphries, 2012; O'Keefe and Nadel, 1978; White & McDonald, 2002), it was surprising that we did not observe a complementary effect of more accurate Cross-route shortcutting in the Distal Group compared to the other two groups of the experiment. It is important to note, though, that the active nature of shortcutting may not offer a good test of whether locally encoded information is embedded within a globally consistent reference frame. Here, successful Cross-route shortcutting can be supported by processes that do not rely on an accurate representation of the spatial structure of the environment. For instance, provided that, at the beginning of a Cross-route wayfinding test, participants headed towards the opposite side of the garden maze, then any errors in their trajectory could be corrected as familiar places that were close to the target location were recognised (Trullier et al., 1997; Warren et al., 2017). Moreover, previous research has demonstrated that the behaviours

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observed during wayfinding tasks are influenced by task instructions (Boone et al., 2019; Redhead et al., 2022), indicating that decisions to shortcut do not only reflect knowledge about the spatial structure of the environment, but also modifiable preferences in wayfinding strategy. Consequently, indices of shortcutting versus route following afford, at best, an indirect and confounded measure of knowledge about the spatial structure of an environment. In contrast, static pointing judgements offer a more sensitive measure of knowledge about spatial structure, because responses measure ability not preference, and cannot be augmented by alternative strategies in the same manner as active wayfinding.

## 8. General Discussion

In Experiments 1a and 1b, participants were required to learn a simple or complex route through a garden maze, respectively, after which they were asked to navigate and point between objects they had encountered along the route. Increasing the complexity of the learned route resulted in worse pointing accuracy on orientation tests, as well as a behavioural shift from flexible shortcutting to route-following and a tendency to become lost more often on wayfinding tests. Surprisingly, though, we observed no benefit of navigating in the presence versus the absence of distal landmarks in Experiment 1a and 1b. In Experiment 2, participants learned the same simple route as in Experiment 1a, but the diagrammatical north and south halves of the route were trained separately. When orientation tests were conducted with objects taken from the separately trained route segments, we observed that the presence of distal landmarks supported better pointing accuracy. However, the presence of distal landmarks did not support better pointing accuracy when objects were taken from within the same route segment, and there were no group differences on any wayfinding tests.

Distal landmarks have been proposed to aid navigation by promoting learning of allocentric spatial relations between objects and places (e.g., O’Keefe & Nadel, 1978; White

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& McDonald, 2002), providing global directional cues to track movement (e.g., Etienne & Jeffery, 2004; McNaughton et al., 1996, 2006), and supporting the planning and execution of novel routes during wayfinding (e.g., He et al., 2022; Redhead et al., 2022). Contrary to these proposals, we were unable to detect a benefit of navigating in the presence of distal landmarks when we assessed participants knowledge of local space, or ability to shortcut through it (i.e., Experiments 1a and 1b, as well as the within-route tests of Experiment 2). Consistent with the proposals of Meilinger (2008), though, we did observe that Cross-route pointing performance was better in the presence versus absence of distal landmarks in Experiment 2. Of course, we cannot conclude that distal landmarks do not promote learning of local spaces on the basis of null results, and it is possible that we may have detected an effect of distal landmarks in Experiments 1a and 1b had we used curved paths or turning angles at intersections that were not always 90°, such that tracking self-motion would be more difficult. Nevertheless, the organised grid structure of our environment is similar to many city environments, and also somewhat reminiscent of the layout of corridors in large office blocks. In these circumstances, our data suggest self-motion cues are sufficient to extract the spatial structure of continuously experienced local spaces, and distal landmarks only supported encoding a spatial representation when behaviour required separately learned segments of an environment to be integrated into a coherent global representation.

In all experiments, we examined individual differences by relating shortcutting and route-following on Shortcut-Available and No Shortcut-Available wayfinding tests, respectively, to pointing accuracy between the same objects. In Experiments 1a and 1b, and the within-route tests of Experiment 2 (Supplementary Section 11.1.3), we observed that pointing accuracy was significantly correlated with the ability to take novel shortcuts, but not related to the ability to follow the trained route. Moreover, in the Cross-route tests of Experiment 2, pointing accuracy correlated with the number of junctions traversed and the

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proportion of perfectly executed shortcuts. Our novel task, therefore, revealed a pattern of data that is consistent with the predictions of parallel memory systems in the cognitive mapping and reinforcement learning literature (Balleine & Dickinson, 1998; Khamassi & Humphries, 2012; Geerts et al., 2020; O'Keefe and Nadel, 1978; Sutton & Barto, 2018; White & McDonald, 2002), in that knowledge about the spatial structure of the environment (measured by pointing accuracy) was necessary for generating flexible navigational behaviours (i.e., novel shortcutting), but not for repeating learned behaviours (i.e., automatic route-following). Whilst this pattern of data may be expected from any parallel memory systems theory, we are not aware of previously published studies that have demonstrated this dissociation using within-subjects measures taken from within the same environment[1].

In contrast to previous studies of individual differences (He et al., 2023; Weisberg & Newcombe, 2016), which have demonstrated that participants can be classified based on their navigational performance, we found little evidence of clustering in our analyses of individual differences. It is relevant to note that, unlike previous studies (Boone et al., 2018, 2019; Furman et al., 2014; He et al., 2023; Marchette et al., 2011), we controlled the payoff for taking novel shortcuts compared to following the trained route across every wayfinding trial. Moreover, pointing responses in the study reported by He et al. (2023) were gathered by giving participants a single fixed view of an object in the environment, and asking them to indicate the direction of another object on an abstract 2D representation space (see also Hilton & Wiener, 2023; Peer et al., 2024). As He et al. noted in their general discussion, this protocol might be particularly difficult for participants with lower spatial ability. In contrast, during our pointing task participants were immersed in the environment and free to orient themselves by rotating their view prior to submitting a response, which may have allowed us to detect the variation that exists between inaccurate and less inaccurate responses. It is possible, therefore, that distinct clusters of performance in previous spatial tasks may reflect

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task-specific variance, such as the payoff for taking a novel shortcut or the (in)ability to translate information acquired from a first-person perspective onto an abstract representation of space, rather than navigational ability per se. These kinds of issues will be important to address in the context of recent calls to develop reliable individual difference measures in the field of spatial cognition (Newcombe, 2023).

There is debate in the current navigational literature as to whether the spatial representations that support wayfinding are encoded in the form of a map or graph, or whether both types of representation are acquired during navigation (see Peer et al., 2021, 2024; Warren, 2019). Theories of cognitive mapping suggest that we encode the spatial relations between places and cues in Euclidean coordinates (Gallistel, 1990; O'Keefe & Nadel, 1978), much like a cartographic map. In contrast, the most basic form of a cognitive graph comprises nodes (places) that are connected by edges (paths) such that the topology of an environment is encoded, akin to maps of the London Underground. Labelled cognitive graphs, however, permit the navigator to learn edge weights and node labels that denote the distance and direction between places, respectively (Warren, 2019). Throughout this report, we have deliberately referred to participants learning the spatial structure of the environment, because our experiments were unable to differentiate the precise nature of the representation participants acquired (i.e., whether participants encoded a map or labelled graph). Our data do, however, permit conclusions about the information contained within any spatial representation that was acquired by participants.

It is informative, here, to contrast our experimental design and findings to recent work that has studied the nature of spatial representations acquired when navigating in open (e.g., a courtyard containing patios, surrounded by distal landmarks) versus closed (e.g., rooms connected by corridors, with no distal landmarks) environments (Peer et al., 2024). In that study, participants learned a virtual environment by navigating along paths to differently

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coloured places (i.e., patios or rooms), and subsequent tests using abstract representations of space probed knowledge about the distances and directions between places in the environment, as well as the lengths of paths connecting places. In a shortest path selection test, participants were told they were standing in one place (e.g., the black room or patio) and presented with boxes that indicated the colours of adjacent places. Participants were then asked to select the colour that offered the shortest path to a target room. On some trials there were two paths that were equivalent in metric length, but differed in the number of intervening places (i.e., one path passed through more patios or rooms than the other path). Here, participants in the closed-maze, and to a lesser extent the open-maze, favoured the route with fewer intervening places, indicating that decisions about the shortest path were based on graph knowledge rather than Euclidean distance (Peer et al., 2024). Whilst the environment for participants in our No Distal conditions was similar to the closed-maze used by Peer et al., our training protocol ensured that participants would only be able to calculate shortcuts had they encoded metric information during training. That is, whilst the training protocol implemented by Peer et al. permitted participants to explore the entire environment, in our paradigm participants were restricted to following the trained route. At test in our experiments, therefore, participants were unaware of the spatial layout of any novel routes, including how many places (junctions) were along them. Consequently, that we observed participants who could point accurately between objects in the environment took novel shortcuts when they were available, indicates that wayfinding decisions in our paradigm were based on knowledge about the distance and direction of the target- from the current-location (i.e., metric information).

The foregoing discussion raises the question as to whether different forms of spatial representation are required to understand navigational behaviours across environments. The data generated from our environments and the open-maze environment used by Peer et al.

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demonstrate that participants encode distances and directions between places, whereas participants were less able to encode this information in the closed-maze used by Peer et al. In the study reported by Peer et al. (2024), open-maze participants performed consistently better than closed-maze participants on all measures, and the authors argued this pattern of data could not emerge if only cognitive graphs were acquired during training, because both open- and closed-maze participants were given the opportunity to learn places (nodes), connections (edges), and directions (node labels). This conclusion, however, rests on an assumption that navigators do not encode distance information (edge weights) in any cognitive graph. If, instead, we assume participants encode distances in cognitive graphs (Warren, 2019), then extant data only permits the conclusion that properties of an environment, and exploration of it (Brunec et al., 2023), determine the accuracy of any spatial representation that is acquired. That is, whilst differences between accurate or less precise representations of the spatial structure of the environment would be apparent on tests of pointing, and potentially flexible wayfinding, the outcome of these tests cannot differentiate navigation based on (less than perfectly metrically accurate) cognitive maps from fully labelled cognitive graphs. Similarly, in less natural circumstances where participants navigate through virtual worlds that violate Euclidean geometry (e.g., Warren et al., 2017) or by teleportation (Peer et al., 2024), it stands to reason that navigators are restricted to learning a topological map or graph as distances and directions are impossible to learn. Extant data, therefore, appears amenable to explanation via maps and graphs, and whilst these are discussed in the literature as distinct spatial representations, future research will need to develop firmer theoretical positions that permit the behaviours based on maps to be truly dissociated from labelled graphs - or we risk debating whether to call a spade a shovel.

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## Footnotes

1. Whilst the design of the present experiments did not differentiate between cognitive mapping and reinforcement learning, recent work in our laboratory has contrasted these theories and provided evidence that navigational behaviours may be better explained under the proposal of reinforcement learning than cognitive mapping (Buckley et al., 2024).

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## CRediT Statement

MGB: Conceptualisation, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – original draft, Writing – review and editing.

JMA: Conceptualisation, Data curation, Funding acquisition, Methodology, Resources, Software, Visualisation, Writing – review and editing.

AM: Conceptualisation, Funding acquisition, Methodology, Supervision, Validation, Visualisation, Writing – review and editing.

## Author Note

The authors have no conflicts of interest to declare. The data presented in this manuscript can be obtained from https://osf.io/e78yf/. Owing to the technical nature of conducting online navigation experiments, in which our programme had to read from and write to our experiment server, it is not possible to make our materials freely available. Use of our online platform may be available upon request.

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## Highlights

- Flexible wayfinding (e.g., shortcutting) requires knowledge of spatial relations.
- Route-following does not require knowing the spatial structure of the environment.
- Shortcutting, but not route-following, was correlated with pointing judgements.
- Distal landmarks did not support learning a spatial representation of local spaces.
- Distal cues supported integrating local spaces in a coherent global representation.

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