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The effects of spatial stability and cue type on spatial learning: Implications for theories of parallel memory systems

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ABSTRACT

Some theories of spatial learning predict that associative rules apply under only limited circumstances. For example, learning based on a boundary has been claimed to be immune to cue competition effects because boundary information is the basis for the formation of a cognitive map, whilst landmark learning does not involve cognitive mapping. This is referred to as the cue type hypothesis. However, it has also been claimed that cue stability is a prerequisite for the formation of a cognitive map, meaning that whichever cue type was perceived as stable would enter a cognitive map and thus be immune to cue competition, while unstable cues will be subject to cue competition, regardless of cue type. In experiments 1 and 2 we manipulated the stability of boundary and landmark cues when learning the location of two hidden goals. One goal location was constant with respect to the boundary, and the other constant with respect to the landmark cues. For both cue types, the presence of distal orientation cues provided directional information. For half the participants the landmark cues were unstable relative to the boundary and orientation cues, whereas for the remainder of the participants the boundary was unstable relative to landmarks and orientation cues. In a second stage of training, all cues remained stable so that both goal locations could be learned with respect to both landmark and boundary information. According to the cue type hypothesis, boundary information should block learning about landmarks regardless of cue stability. According to the cue stability hypothesis, however, landmarks should block learning about the boundary when the landmarks appear stable relative to the boundary. Regardless of cue type or stability the results showed reciprocal blocking, contrary to both formulations of incidental cognitive mapping. Experiment 3 established that the results of Experiments 1 and 2 could not be explained in terms of difficulty in learning certain locations with respect to different cue types. In a final experiment, following training in which both landmarks and boundary cues signalled two goal locations, a new goal location was established with respect to the landmark cues, before testing with the boundary, which had never been used to define the new goal location. The results of this novel test of the interaction between boundary and landmark cues indicated that new learning with respect to the landmark had a profound effect on navigation with respect to the boundary, counter to the predictions of incidental cognitive mapping of boundaries.

1. Introduction

An appealing hypothesis for how humans and non-human animals navigate is that they encode a map of their environment, in which the locations of important places and environmental cues are represented. According to cognitive mapping theories (e.g. O'Keefe & Nadel, 1978), a locale system based in the hippocampal formation is responsible for generating an allocentric map of the environment, in which metric relations among stimuli are represented, and by which novel trajectories between locations can be plotted (Zhou & Mou, 2016, 2018; Bellmund, de Cothi, Ruiter, Mau, Barry, & Doeller, 2020). A complex network of grid, head-direction and place cells in the hippocampal formation form

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the basis of the cognitive map (review in Poulter, Hartley, & Lever, 2018), and environmental geometry strongly influences the firing patterns of both place cells (O'Keefe & Burgess, 1996; Krupic, Bauza, Burton, & O'Keefe, 2018) and grid cells (Krupic, Bauza, Burton, Barry, & O'Keefe, 2015; Stensola, Stensola, Moser, & Moser, 2015; review in Krupic, Bauza, Burton, & O'Keefe, 2016). A parallel, non-hippocampal formation system, is responsible for learning about explicit sensory cues (McGregor, Hayward, Pearce, & Good, 2004; Morris, Garrud, Rawlins, & O'Keefe, 1982) or routes through the environment based on a sequence of stimulus-response associations (Packard & McGaugh, 1996). This taxon system is thought to be less flexible than the cognitive map, meaning that taxon-based navigation is fixed and rather rigid.

A number of neuroimaging studies have supported the notion that cognitive mapping of space recruits the hippocampus (Aguirre, Detre, Alsop, D'Esposio, 1996; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003; Maguire et al., 1998; Marchette, Bakker, & Shelton, 2011). However, there is growing evidence that metric relations among stimuli can be learned independent of the hippocampus (Bohbot et al., 1998; Maguire, Nannery, & Spiers, 2006; Pearce, Roberts, & Good, 1998) with particular emphasis on the role of the striatum in such learning (Doeller, King, & Burgess, 2008; Kosaki, Poulter, Austen, & McGregor, 2015). For example, building on the finding that cells responsible for the development of a cognitive map are sensitive to the geometric properties of the environment, Doeller et al. (2008) used fMRI to show that learning object locations relative to a circular boundary activated the hippocampus, but that learning object locations relative to a landmark activated the dorsal striatum.

A key prediction of cognitive mapping theory (O'Keefe and Nadel, 1978) is that learning in the locale system occurs as a function of exploration of the environment, so that as new information is encountered it is incorporated into the map. This incidental learning is thought not to be subject to prediction error as stipulated in theories of associative or reinforcement learning (e.g. Rescorla & Wagner, 1972; Sutton & Barto, 1998), and so should not be susceptible to cue competition effects such as overshadowing (Pavlov, 1927) and blocking (Kamin, 1969), in which learning about on one cue is restricted, or prevented, by learning about another cue. In light of evidence for dissociable hippocampal and striatal memory systems for learning based on boundaries and landmarks, respectively (Doeller et al., 2008), Doeller and Burgess (2008) sought to examine cue competition effects between these different types of spatial cues in humans. Participants were trained to collect four objects within a virtual environment that was always orientated by distal cues. These cues were rendered at infinity so they could not be used to determine distance, only orientation. Participants were placed within a circular arena bounded by a uniform wall, and within the arena there was a rotationally symmetrical landmark. Two of the four objects always remained in the same locations relative to the boundary, whereas the other two objects remained stable in terms of a vector from the landmark, but unstable with respect to the boundary because the landmark moved within the arena across blocks of trials. Having collected the objects, participants replaced them one at a time in their previous positions, and performance was measured by the distance error between where each object was replaced and its original position. In a subsequent compound learning stage, training continued with the landmark now in a fixed position across trials such that both the boundary and landmark predicted the location of every object in the environment. This compound stage was crucial for determining if learning based on boundaries or landmarks was governed by either an incidental or an error-correcting associative learning rule. According to associative learning theories, prior training should block subsequent learning in the compound stage of the experiment, even though the boundary or landmark becomes relevant for locating the position of the object. In contrast, incidental encoding in the cognitive map should mean that the cue that becomes relevant in the compound stage is learned about. To test this, participants were given probe trials in which they were asked to replace an object in the presence of just the landmark or boundary. When replacing objects that had been related to the boundary throughout training, but only related to the landmark during the compound stage, it was observed that distance error was greater when participants were tested with the landmark cue than when tested with the boundary. In contrast, when replacing the objects that had been related to the landmark in the first training stage, and to both cues in the compound stage, there was no difference in distance error between tests conducted with the landmark or boundary cues.

According to Doeller and Burgess (2008), their results demonstrated that prior learning with respect to the boundary associatively blocked subsequent learning based on the landmark. In contrast, learning an object's location with reference to a landmark had no subsequent effect on learning with reference to the boundary. These results support the notion that locale learning based on the boundary was governed by an incidental learning rule, whereas taxon learning based on the landmark was subject to an error-correcting learning rule: a pattern of data that fits with the memory systems that are associated with learning with respect to boundaries and landmarks (Doeller et al., 2008). However, while Doeller and Burgess's (2008) results appear to support a parallel spatial memory systems account, there is an important discrepancy between how they were interpreted in relation to more traditional cognitive mapping theories. In traditional formulations of cognitive mapping theory, in which relations among stimuli in the environment are coded (O'Keefe & Nadel, 1978), there is no stipulation of what cue type (e.g. boundary or landmark) can be encoded in the cognitive map (see discussion in Lew, 2011). In contrast to this theoretical viewpoint, Doeller and colleagues (Doeller et al., 2008; Doeller & Burgess, 2008) argued that boundaries are encoded incidentally in the locale mapping system, whereas any configuration of landmarks is encoded associatively in the taxon system.

While the emphasis on the role of boundaries in cognitive map formation was driven by evidence of their importance for predicting the properties of grid cells and place cells discussed above, some results seem to contradict the cue-type formulation of the parallel memory systems theory (Doeller & Burgess, 2008). For example, in rats, Kosaki et al. (2015) found that lesions to the dorsolateral striatum impaired navigation with respect to a landmark, but that they facilitated memory for a cognitive map of the distal cues in the environment. Poulter et al. (2019) found the reciprocal effect when lesions to the hippocampus facilitated learning based on landmarks. These data have been interpreted as evidence that the hippocampal and striatal systems do not necessarily operate in parallel. Instead, in intact animals, hippocampus-based memory for a cognitive map competes with striatum-based memory for the landmark, and there is a release from this competition when one of the systems is impaired. Moreover, in humans, using the Doeller and Burgess paradigm, patients with hippocampal atrophy were severely impaired in learning both landmark-related and boundary-related goals, against predictions that learning with respect to a landmark would be possible without hippocampal involvement (Guderian et al., 2015). And in a neuroimaging study, Wegman, Tyborowska, and Jansen (2014) found that coding a goal location with respect to a landmark array was associated with hippocampal activation, relative to coding to a single landmark which was associated with striatal caudate activation. Again, these findings suggest that it is not the type of cue that that matters in the parallel memory systems framework, but how they are processed (White & McDonald, 2002).

Behavioural evidence has also questioned whether learning based on boundaries is always immune from cue competition (Buckley, Smith, & Haselgrove, 2019; Zhou & Mou, 2019). Zhou and Mou (2019) recently manipulated the position of a landmark in a circular arena in an overshadowing task, similar to that of Doeller and Burgess (2008; experiment 1). When the landmark was centrally placed the results replicated Doeller and Burgess (2008), but when the landmark was more peripheral, close to the boundary, then the boundary was overshadowed by the landmark. Therefore the immunity of boundaries to cue competition is has already been shown to be parameter dependent, and the generality of such a finding is thus in doubt.

One possible resolution to the apparent contradictory formulation of traditional cognitive mapping theory (O'Keefe & Nadel, 1978), and one based on cue-type (Doeller & Burgess, 2008), is from the observation that the landmarks in many spatial paradigms are made spatially unstable, assuming the boundary is perceived as remaining stable, by moving them within the arena between trials. Stability has been argued to be a critical variable in recruiting mapping systems (O'Keefe & Nadel, 1978, p. 95, see also Kneirim & Hamilton, 2011), and some behavioural studies have demonstrated that spatial learning is only possible when landmarks are geometrically stable (Biegler & Morris, 1993, 1996; Cheng, 1988). Although subsequent studies showed that stability was not a prerequisite for spatial learning per se (Hogarth, Roberts, Roberts, & Abroms, 2000; Leising, Hall, Wolf, & Ruprecht, 2015; Roberts & Pearce, 1998), it was later found that learning based on an unstable landmark did not require a functioning hippocampus (Pearce et al., 1998) but did require the dorsolateral striatum (Kosaki et al., 2015; see also Auger, Mullally, & Maguire, 2012; Auger, Zeidman, & Maguire, 2015, 2017 for evidence of neural sensitivity to spatial stability in humans). In a number of studies that have examined cue competition between boundaries and landmarks, the boundaries of the arena are always stable, whereas the landmarks are unstable. For instance, in the experiment conducted by Doeller and Burgess (2008), the symmetrical boundary would appear to be stable in relation to the orientation cues, but assuming the boundary is perceived as being stable (Epstein, Patai, Julian, & Spiers, 2017) the landmark would appear to move relative to the boundary between trials. Moreover, it is possible that the parameter-dependent overshadowing of boundary learning by a landmark (Zhou & Mou, 2019 - see above) was partly driven by the perceived stability of the cues in the environment, with it being easier to detect the stability of the landmark in relation to the boundary when it was placed close to the arena walls (i.e., placed peripherally) compared to when it was further from the arena walls (i.e., placed centrally). Since the key prediction of cognitive mapping theory, that spatial learning in the locale system should progress incidentally as a result of exploration (O'Keefe & Nadel, 1978, p. 94), flows directly from an expectation that objects in the cognitive map are geometrically stable, it is problematic when experimental designs conflate cue stability with cue type (see also Buckley et al., 2019; Graham, Good, McGregor, & Pearce, 2006; Hayward, McGregor, Good, & Pearce, 2003). In the experiments reported here, therefore, we investigate whether the spatial stability of cues, rather than cue type, would determine whether cognitive mapping is subject to cue competition effects.

We designed four experiments in which we manipulated the stability of boundaries and landmarks during initial learning. Participants were first trained to learn two locations, one of which was in a fixed position in relation to the boundary, and the other in a fixed position in relation to a landmark. For the boundary stable group, the landmarks within the environment moved between trials in the initial training phase, whereas the boundary remained in a fixed position. For the landmark stable group, the boundary walls of the environment moved between trials during initial training, and the landmark remained in a fixed position. Following this initial training, participants then received compound training in which all cues within the environment were stable, and predicted both goal locations. To detect blocking of learning during the compound phase, participants were given four probe trials in which, unknown to the participants, the opportunity to find the hidden goal was removed, and the time spent searching in the region of the environment where the goal was located during training was recorded as a measure of learning. Two of these probe trials were blocking probes, in which participants were instructed to search for the goal using the cue that had become predictive only during compound training. The remaining probes were control probes, in which participants were instructed to search for the goal with cues that had been predictive throughout all stages of the experiment. Blocking for a given goal would, therefore, be indicated by participants spending less time in the relevant region during blocking probes relative to control probes.

According to the cue-type hypothesis, a special status is afforded to boundary cues over landmark cues, irrespective of their stability. Consequently, initial learning about the location of the boundary-related goal with respect to boundary should block subsequent learning about the location of that goal with respect to landmarks during compound training. In contrast, learning the location of the landmark-related goal with respect to landmarks should not block learning about the location of that goal with respect to boundary in the compound phase. If cue-stability is a critical variable in recruiting mapping systems, a special status is afforded to cues that remain in a constant position within the environment, regardless of whether they are boundary or landmark cues. Consequently, initial learning with respect to boundaries should block learning about landmarks during the compound phase only in the boundary stable condition. In the landmark stable condition, initial learning with respect to landmarks is anticipated to block subsequent learning about the boundary during compound training. Importantly, initial learning about the unstable cue should not block learning about the stable cue during compound training. A third possibility is that neither cue type nor cue stability modulate blocking. Instead, as predicted by domain-general theories of associative learning, prior training with either a landmark or boundary, regardless of stability, will result in reduced learning based on the added cue during compound training.

2. Experiment 1

In keeping with traditional tests of spatial learning in rodents (e.g., Morris, 1981), and more contemporary research conducted with humans using virtual environments (e.g., Astur, Taylor, Mamelak, Philpott, & Sutherland, 2002), we used a goal-finding procedure in which participants were trained to locate invisible goals during training before removing the opportunity to find the goal at test. In such paradigms, the time spent searching in a zone centred on the goal location at test is taken as a measure of what participants had learned about the location of the hidden goal during training. This choice differed from the object-location procedures reported by Doeller and Burgess (2008) and Mou and Zhou (2013); however, both tasks require that participants learn multiple target locations in an environment, and our manipulations controlled which cues were relevant for different goals, as was the case for objects in the paradigm reported by Doeller and Burgess (2008). We chose a goal-finding task to increase motivation, because during training participants had to remain in the trial for more than 60s if they failed to locate the hidden goal. In contrast, in an object location task replacing the object would take a participant around 10s per trial, and the cost to inaccurate performance is low. We speculated that the high cost of inaccurate performance in our task would increase the strength of learning in the first phase of training, thereby maximising the sensitivity of the task in terms of detecting a blocking effect.

During Experiment 1, participants were required to locate invisible Wi-Fi and mobile signals that were located within a virtual c-shaped environment that contained a single wind-turbine (see Fig. 1). This entire environment was orientated by 4 distal orientation cues that remained in a constant position throughout the experiment. The C-shaped boundary was designed to be as similar as possible to the Doeller and Burgess (2008) environment, while being asymmetric so that instability could be detected when the boundary rotated between trials (see below). The intra-boundary placement of the single landmark was also designed to follow as closely as possible the environment used in Doeller and Burgess, while being asymmetric, to mirror the asymmetric boundary shape.

During initial training for the Boundary Stable group, the C-shaped wall remained in the same orientation between trials, relative to the distal cues, while the wind-turbine moved relative to the boundary between trials. Conversely, for the Landmark Stable group, the wind-turbine remained static, but the boundary walls rotated relative to

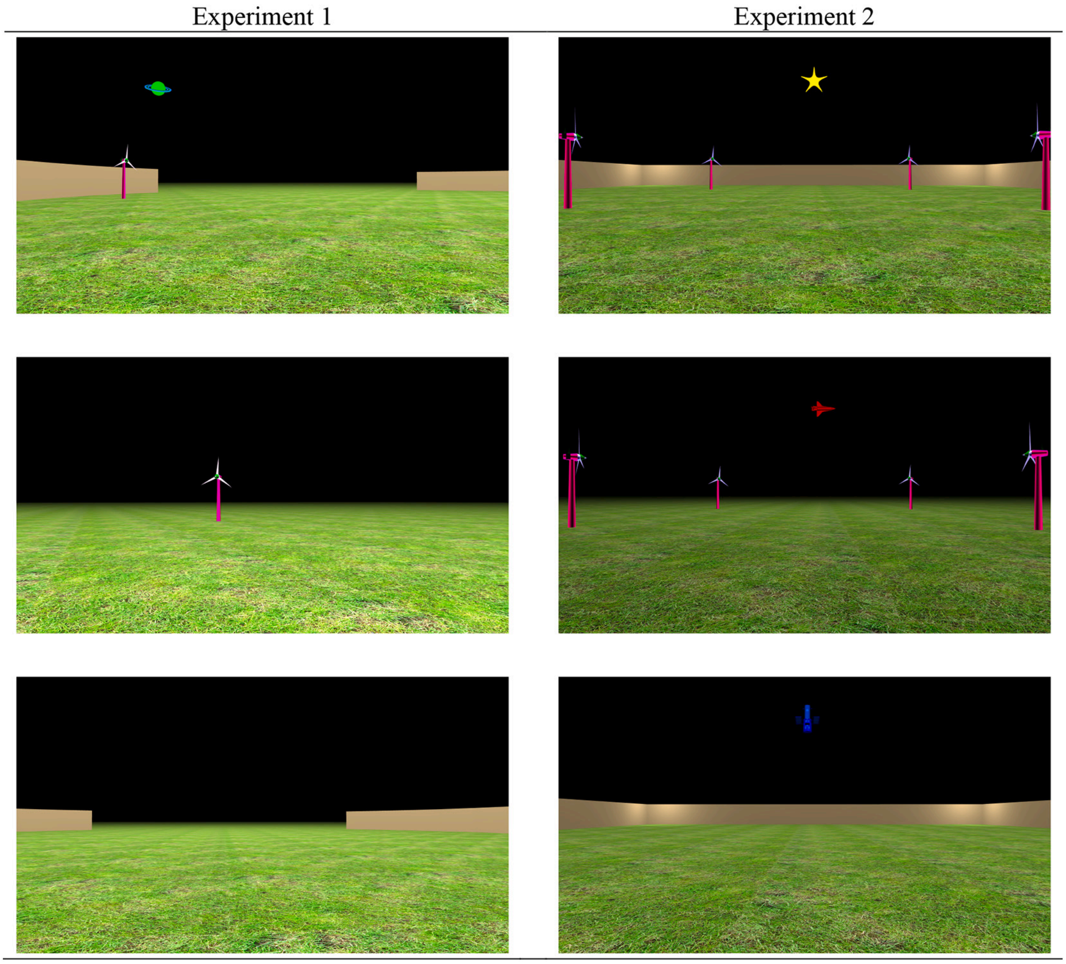

Fig. 1. Views of the experimental environment in Experiments 1and 2 from the participant's perspective, showing the boundary and landmark cues in addition to the distal orientation cues. The upper panels show the environments during the compound training stage in Experiments 1 (upper left) and 2 (upper right). The different distal cues reflect the participant facing in different directions in different panels. The middle panels show the environments during probe trials when only landmarks were present (together with distal cues in Experiment 2), and the lower panels show the environments during probes trials with only the boundary present (together with distal cues in Experiment 2).

both the landmark cue and orientation cues between trials. During initial training in both groups, one of the signals maintained a constant relation with the boundary wall of the environment (boundary-related goal), whilst the other signal maintained a constant relation with the wind-turbine (landmark-related goal).

Following initial training, participants received compound training in which all cues in the environment remained in a constant position with respect to one another. The location of each of the goals could therefore be determined by both the boundary and landmark cues. The two signals were located equidistant from the boundary and landmark cues to avoid distance confounds. Probe trials, in the absence of the opportunity to locate the goals, were presented at the end of the compound training phase to determine if blocking had occurred. To index learning about the boundary or landmark cues only, probe trials were also conducted without the four orientation cues, as the boundary and landmark cues provided directional information by their asymmetric nature. As outlined in the introduction, the cue-type hypothesis predicts learning with respect to the boundary will block learning with respect to the landmark in both groups, whereas the cue-stability hypothesis predicts learning with respect to stable cues will block learning with respect to unstable cues.

2.1. *Method*

2.1.1. *Participants*

32 participants (18 female) from Durham University took part in the experiment, and were given course credit in return. Participant ages ranged between 19 and 35 ($M = 23.84$, $SD = 3.14$). Ethical approval was obtained from the Department of Psychology Ethics Committee, Durham University, and the research was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). Informed consent was obtained from each participant in this experiment and all of the others reported in this article.

2.1.2. *Materials*

All virtual environments were created and displayed using MazeSuite (v 2.6) software (Ayaz, Allen, Platek, & Onaral, 2008; mazesuite.com), which ran on an Apple MacBook Pro (A1502) under a Windows 10 partition. Participants viewed the virtual environments from a first-person perspective, with a field of view set to 45° in MazeSuite, on a large (52.07 × 92.71 cm) Sony Bravia (KDL-43W809C) television. Assuming a walking speed similar to that in the real world (2 m/s), the diameter of the c-shaped environment was 30 m. As shown in Fig. 1, a grass texture was applied to the 780 m × 780 m ground of the arena, and the sky rendered as a uniform black expanse. The environment was lit by a single light source placed 18 m above the centre of the arena floor. The 3 m-high walls of the environment were cream coloured, and defined as

204, 178, 127 using the 0–255 RGB scale employed by MazeSuite.

Four orientation objects were placed at notional cardinal points of the environment, and rendered at infinity. In clockwise order, these objects were models of a planet, the Hubble space telescope, a star, and a spaceship. The location of these objects was counterbalanced across participants by rotating the configuration of four cues, such that each object held the north position for four participants within each group. In addition, a 4 m-tall wind-turbine acted as the intra-maze landmark, and a mobile phone and internet router were used during the training trials of the experiment to indicate the goal locations (see 2.1.3 Procedure). The spaceship and Hubble telescope models were obtained from nasa.gov, whilst all other models were downloaded from turbosquid.com. The size and colour of all objects were modified using Blender software (blender.com), before being imported into MazeSuite.

The landmark-related and boundary-related goals were square-shaped goal regions (2.14 m × 2.14 m) that were invisible to participants. During Stages 1 and 2, the boundary-related goal maintained a fixed vector from one edge of the wall. Similarly, the landmark-related goal maintained a fixed vector from the wind-turbine within the environment. In the compound stage of the experiment, these vectors remained unchanged and each goal was equidistant (4.75 m) from the landmark and boundary (see Fig. 2).

2.1.3. Procedure

Participants gave written consent after reading a standard set of instructions (Appendix A) prior to beginning the experiment. Each participant sat not more than 1.5 m away from the screen with a keyboard on their lap. Before training began, participants were given a single exploration trial in which they were allowed to walk around the experimental environment used for compound training in both groups (but without goal locations present – see below) for 60s in order to familiarise themselves with the controls. Presses on the “up” and “down” cursor keys permitted the participant to move forwards and backwards within the arena, respectively, while presses on the “left” and “right” cursor keys permitted the participant to rotate counter-clockwise and clockwise within the environment, respectively. In addition to receiving the instructions at the start of the experiment, participants were re-presented with the relevant part of the instructions (Appendix A) on screen at the onset of Stage 1 and Stage 2 training. The purpose of these instructions was simply to ensure participants understood the task in early trials of the experiment; thus, following the onset of stage 2 training, trials began automatically, without any further instruction being provided.

Throughout the experiment, participants were required to find either a mobile or Wi-Fi signal, which served as the landmark- and boundary-related goals. Participants were cued to search for a particular signal by displayed text (e.g. *find the mobile signal*) for 2 s at the beginning of each trial. There was no time limit for any training trials, thus, each trial ended only when the hidden goal was found. Once the hidden goal had been found, participants could no longer move and a congratulatory message (e.g. *Mobile signal found!*) was displayed on screen. Participants pressed the “enter” key to begin the next trial.

During Stage 1 training the locations of the hidden goals were indicated to the participants by the presence of a mobile phone and internet router on the floor of the environment. During stage 2 training the location of each signal was only indicated to participants if they did not locate it within 60s, at which point a mobile phone or Wi-Fi router (whichever was the goal for that trial) appeared in the appropriate place in the environment to signal the location of the goal. For the Boundary Stable group in Stages 1 and 2, the c-shaped wall maintained a stable relation with the orientation cues. In contrast, the landmark moved between trials such that it was located near each of the four orientation cues across training, relative to the boundary. For the Landmark Stable group in Stages 1 and 2, the landmark maintained a stable relation with the orientation cues. In contrast, the c-shaped boundary rotated between trials relative to the orientation cues in increments of 90°, such that

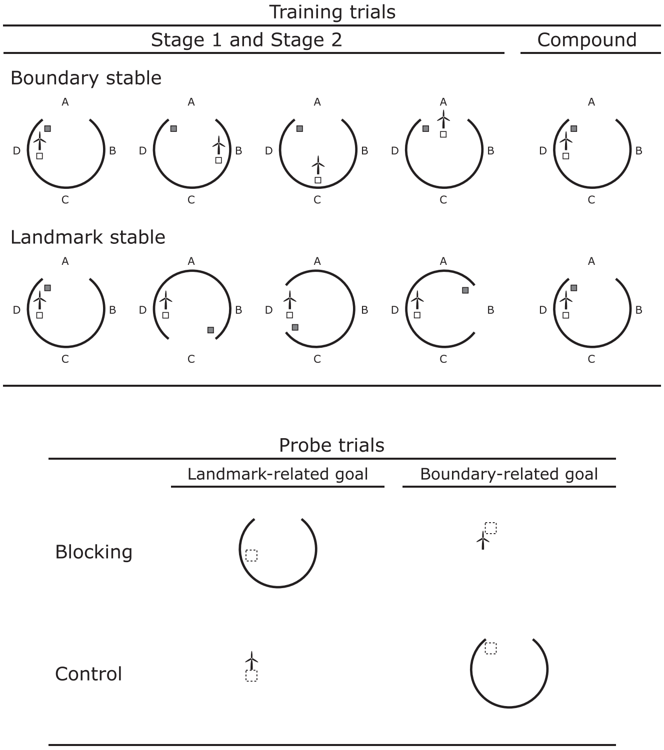

Fig. 2. An example of the trials given to the Boundary Stable and Landmark Stable groups during Stages 1–3 (upper panel) and in Probe trials (lower panel) for Experiment 1. The boundary-related goal is shown as a grey square, and the landmark-related goal as an open square. The distal orientation cues are lettered. During the Probe trials the goals were removed and time spent searching in the goal zones, shown as dotted squares for every goal zone, was recorded.

middle of the gap in the wall faced directly north, south, east, and west (see Fig. 2).

To discourage learning based on a fixed egocentric route, which could interfere with mapping of the environment (Morris, 1981; Poulter et al., 2019; Whishaw & Mittleman, 1986), participants in both groups began Stage 1 and 2 training trials from one of 4 locations, facing in a randomised direction. For the Boundary Stable group, when locating a given goal, participants began one trial from each of the four different start locations for each landmark position described previously. This generated 16 boundary-related goal trials, four of which were used in Stage 1 training, with the remaining 12 used in Stage 2 training. When locating the boundary-related goal, participants in the Landmark Stable group began one trial from each of the four different start locations for each of the four orientations of the boundary described previously. The same process was used to create landmark-related goal trials for this group. Again, this generated 16 trials different trials for each goal, which were then spread across Stage 1 and 2 training as described above. The order of trials for both groups was pseudo-randomised to ensure that participants were not asked to find either the landmark- or boundary-related goal on more than two consecutive trials. In addition, within a block of four trials participants began once from each start location.

In Stage 3, participants received compound training in which all cues were stable with respect to the distal orientation cues, and both signals within the environment were equidistant from the boundary wall and the landmark. As with Stage 2, the goal locations were not indicated to participants unless 60s of a trial had elapsed. For the Boundary Stable group, each of the four landmark positions was used once in this stage, counterbalanced between-subjects. For the Landmark Stable group, each of the four boundary orientations was used once in this stage, counterbalanced between-subjects. In both groups, participants began one trial from each of the four different start locations.

Having completed training (4 trials in Stage 1, 12 in Stage 2, and 4 in Stage 3), participants received four probe trials in which they navigated with either the landmark or boundary cues for 60s. The hidden goal was not present on probe trials, and participants were instructed to search for either the Wi-Fi or mobile signal, as appropriate. Performance during each probe was recorded by measuring the time participants spent searching in a square search zone, with side lengths double that of the goal (4.28 m), the centre of which was aligned with the centre of goal location during training. Participants began each probe trial in a novel position at the centre of the arena, facing in a random direction. In blocking probes participants were required to find the goal that was related to the boundary (boundary-related goal) in stages 1 and 2, using only the landmark cue, and the goal related to the landmark position (landmark-related goal) in stages 1 and 2, using only the boundary. In control probes, participants were required to find a goal using the cue to which it was related throughout training, including Stages 1 and 2. So participants were required to find the boundary-related goal with the boundary, and the landmark-related goal with the landmark.

Crucially, administering the blocking and control probes in the order described above avoided confounding blocking with extinction. That is, any extinction of behaviour due to the absence of goals in the probe trials would impact the control probes more than the blocking probes, reducing our chance of observing a blocking effect. Since probe trials were not reinforced, there was no opportunity for participants to learn any other cue-specific details in these trials. The order of the two blocking probes was counterbalanced across participants, as was the order of the control probes.

2.2. Results

For all statistical tests reported, we adopted an alpha level of 0.05. Interactions were analyzed with simple main effects analysis using the pooled error term from the original ANOVA. Where sphericity of within-subjects variables could not be assumed, a Greenhouse-Geisser correction was applied. Alongside the results of each null-hypothesis significance test, we report estimates of effect size, and, where appropriate, confidence intervals around that effect size in order to communicate uncertainty in the data (Lakens, 2013; Steiger, 2004: see also Buckley et al., 2016a).

2.2.1. Stage 1

It is important to note that direct comparisons between latencies to locate the landmark-related goal and boundary-related goal should be made with caution because the distance from the start location to the goal location differed depending on which goal was being sought on a given trial. The boundary-related goal was necessarily located at the periphery of the environment which could have resulted in longer latencies for the boundary- than the landmark-related goal. Accordingly, we limited any post-hoc analyses, here and elsewhere, to comparisons between training conditions for each goal separately. We also calculated the mean of each set of four trials so that the average distance to the goal from the start location, for boundary-related and landmark-related goals separately, was equated within a block of four trials. The left side of the top panel of Fig. 3 shows the mean latencies to find the boundary- and landmark-related goals for both the Boundary Stable and Landmark Stable groups when the goals were visible. There were no significant differences between groups in the time taken to locate either the boundary-related goal, $t(30) = 0.24$, $p = .81$, Cohen's $d = 0.08$ [−0.60–0.78] or the landmark-related goal, $t(30) = 0.11$, $p = .91$, Cohen's $d = 0.04$[−0.66–0.73].

2.2.2. Stage 2

The middle of the top panel of Fig. 3 shows the mean latencies to find the boundary- and landmark-related goals for both the Boundary Stable and Landmark Stable groups when the goals became invisible. A two-way ANOVA of individual latencies to find the boundary-related goal, with a between-subjects variable of group (Boundary Stable or Landmark Stable) and within-subjects variable of block (1–3), revealed a significant main effect of block, $F(2, 60) = 18.25$, $p < .001$, $\eta_p^2 = 0.38$ [0.21–0.49], but no effect of group, $F < 1$, and no interaction between the main effects, $F < 1$. The same analysis for the landmark-related goal showed very similar results, with a main effect of block, $F(2, 60) = 10.63$, $p < .001$, $\eta_p^2 = 0.26$ [0.10–0.39], but no effect of group, $F < 1$, and no interaction, $F(2, 60) = 2.00$, $p = .17$, $\eta_p^2 = 0.06$ [0.00–0.16].

2.2.3. Stage 3

The right side of the top panel of Fig. 3 shows the mean latencies to find the boundary- and landmark-related goals for both groups during compound training. There were no significant differences between groups in the time taken to locate either the boundary-related goal, $t(30) = 0.60$, $p = .56$, Cohen's $d = 0.21$ [−0.49–0.90], or the landmark-related goal, $t(30) = 0.27$, $p = .79$, Cohen's $d = 0.10$ [−0.60–0.79].

2.2.4. Probes

The lower panel of Fig. 3 shows the mean time that participants spent searching within the zone surrounding the goal location during blocking and control probes. The results for the Boundary stable group are shown in the left lower panel of Fig. 3 and equivalent result for the Landmark stable group in the right lower panel. Both show a similar pattern, neither of which is consistent with both the cue-type and cue-stability hypotheses. Two-way ANOVAs of individual time spent in zone, with within-subjects variables of test cue (landmark or boundary) and goal (landmark-related or boundary-related) for both the Boundary Stable and Landmark Stable groups showed interactions between the main effects in both analyses, $Fs\ (1, 15) > 32.95$, $ps < 0.001$, $\eta_p^2s > 0.69$ [0.39–0.79], but no effects of either goal or cue in either analyses, $Fs\ (1, 15) < 1.92$, $ps > 0.1$, $\eta_p^2s < 0.11$[0.00–0.36].

2.3. Discussion

The purpose of Experiment 1 was to examine whether cue-type or

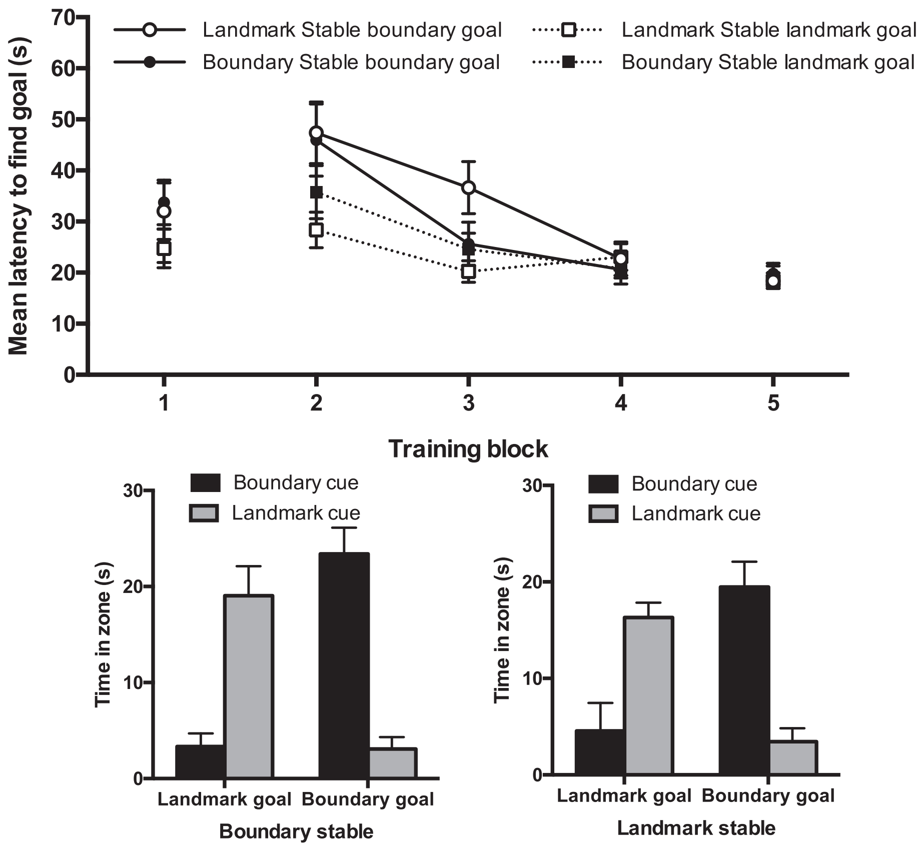

Fig. 3. Upper panel: Mean latencies (± one standard error) for both Boundary Stable and Landmark Stable groups to find the goal during training in Experiment 1. Data are shown in four-trial blocks. Block 1 corresponds to stage 1 training in which the goals were visible. Blocks 2–4 correspond to stage 2, and block 5 to stage 3. Lower panel: The mean percentages of time (± one standard error) spent in the search zones for the Boundary Stable (left) and Landmark Stable (right) groups during the Probe trials of Experiment 1.

cue-stability modulate blocking in spatial learning. In Doeller and Burgess's (2008) experiment, it was observed that object locations were always learned about with respect to the boundary of an arena, despite a prior training stage in which only an unstable landmark predicted an object location. The results were interpreted in terms of a special incidental learning rule for environmental boundaries consistent with the action of a hippocampus-based cognitive map (Doeller et al., 2008). An alternative to this interpretation is that it was not the cue type that was the subject of the incidental learning rule but rather the perceived stability of the boundary in comparison to the landmark (see introduction). Therefore, in the current experiment the stability of both the landmark and the boundary was manipulated within a blocking design. When searching for both the landmark- and boundary-related goals, participants in both the Boundary Stable and Landmark Stable groups spent more time searching in the goal zone when tested with the cue that was initially predictive of the goal's location (control probes) than with the cue that was later introduced as predictive (blocking probes). These data indicate that learning a goal location with respect to a boundary blocks subsequent learning about the goal location with respect to a landmark. Similarly, initial learning with respect to a landmark blocks subsequent learning about a boundary. The results also indicate that cue stability had no effect on blocking.

The results of the current experiment are counter to the predictions of both the cue type account (Doeller & Burgess, 2008) and cue stability account (Biegler & Morris, 1993; O'Keefe & Nadel, 1978), both of which suppose that learning should be immune to blocking under some of the conditions in Experiment 1. While the results are surprising, given the predictions based on prior research, they are consistent with an account based on the principles of associative learning, in which all cues are permitted to compete with each other for control of spatial behaviour (e.g., Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972). Before accepting this associative explanation, however, it is necessary to consider differences between the environment used in our experiment compared with that of Doeller and Burgess (2008), who found very different results. It is possible, for example, that the use of asymmetric boundary and landmark cues in the current experiment did not provide a fair test of the cue-stability hypothesis. Given their asymmetry, it was possible for participants to orient using the boundary or landmark cues alone in our task and, consequently, participants in either the Boundary Stable or Landmark Stable groups may not have attended to the distal orientation cues. There is support for this conclusion as the probe trials were conducted in the absence of the distal cues, and participants were still able to navigate to the goal locations in the control conditions. This is problematic, as it was intended that the stability of landmark and boundary cues in the Landmark Stable and Boundary Stable group, respectively, should be defined by their relationship relative to the static orientation cues. If these orientation cues were ignored by participants, then it is possible that both the landmark and boundary cues appeared unstable for both groups. If this were the case, the cue-stability hypothesis would predict that landmark and boundary cues that were perceived to be unstable would be subject to associative cue competition. Therefore, the cue-stability hypothesis would anticipate the reciprocal blocking effect that was observed here. Arguably, however, in the case of the boundary cues it would seem likely that ignoring the orientation cues would cause the unstable boundary to appear stable as orientation and boundary are conflated in this case, which would still make the finding that the (unstable) landmark blocked the (stable) boundary a problem for the conclusions of Doeller and Burgess (2008). Regardless of the merits of this analysis, to assess whether it is the role of the orienting cues that determines the asymmetric blocking effect obtained by Doeller and Burgess, it was necessary to conduct a second experiment. In Experiment 2 we made the landmark and boundary cues symmetrically ambiguous meaning participants were required to refer to the orientation cues to locate the goals effectively.

3. Experiment 2

The purpose of Experiment 2 was to assess if the reciprocal blocking effect that was observed in Experiment 1 would replicate under conditions in which the distal orientation cues had to be referred to for effective navigation. This was achieved by making both the boundary and landmark cues directionally ambiguous, which we hypothesised would increase the opportunity for an incidental learning rule to control behaviour in the boundary learning condition. Participants were again required to find boundary- and landmark-related goals, this time within a square-shaped environment that contained a square array of four identical landmarks, oriented by four distal cues. As in Experiment 1, for the Boundary Stable group the arena walls did not vary between trials, so the boundary-related goal was in a stable location, but during initial training the landmark array moved relative to the boundary cues between trials, so the landmark-related goal appeared to be unstable. For the Landmark Stable group, the square array of landmarks remained in a constant position during initial training while, following Doeller and Burgess (2008, Experiment BB), the boundary walls were made unstable by increasing and decreasing their lengths between trials.

A square was chosen because not only would varying its dimensions create an unstable environment, but also a goal location could be coded with respect to one of its corners. Zhou and Mou (2016, 2018) showed that participants learned a vector from the nearest point in the arena, so we fixed the boundary-related goal relative to the nearest corner. If a circular boundary had been used and its diameter varied between trials, the question of how to define the boundary-related goal location would have arisen. This is because there are an almost infinite number of vectors that be drawn from a circular wall to a goal location (Mou & Zhou, 2013) and, if we placed the boundary-related goal perpendicular to a tangent from the nearest point on the boundary to the goal, a fixed distance from the wall, then its position with respect to every other vector drawn from the circle would alter between trials. Whilst it would be mathematically possible to define a boundary-related goal location with respect to a single vector in an unstable circular boundary, it would have been near impossible for participants to selectively encode this vector from among an infinite number of possible vectors. Although one experiment by Doeller and Burgess (2008, Experiment BB) varied boundary size, therefore changing the vector between trials, such a manipulation would have had a more minor effect in their study as participants were required to replace an object in an approximately correct location, rather than learn the precise location of a hidden goal. Therefore, being imperfect in their study would have had a smaller effect than being imperfect in ours, in which participants had to navigate to a precisely defined goal region to terminate trials.

The inclusion of the square landmark array was partly to maximise similarity between cue types, and partly to ensure that different points of the landmark array (i.e., landmarks further from the goal location) defined the boundary-related goal location during compound training similarly to the different corners of the square boundary. Therefore, the symmetry of the cues in Experiment 2 ensured that spatial search was controlled by the calculations of vectors in the same way as achieved by Doeller and Burgess (2008), and our choice of cues achieved the same dissociation between distance and directional vector components that were based on the proximal (landmarks or boundary) and distal orientation cues, respectively.

Following initial training, participants in both groups received compound training in which all cues remained in a constant position, such that both goal locations could be defined with both cue types. Finally, participants received blocking and control probes to assess blocking of learning during the compound phase. In keeping with Experiment 1, the hidden goal was removed from the environment during probe trials. However, in contrast to Experiment 1, the orientation cues were present in Experiment 2. As before, blocking for a given goal would be indicated by participants spending less time in the region surrounding the goal location during blocking probes relative to control probes.

3.1. Method

3.1.1. Participants

32 participants (28 female) from Durham University took part in the experiment, and were given course credit in return. Participant ages ranged between 18 and 22 ($M = 19.69$, $SD = 0.97$).

3.1.2. Materials

Unless detailed here, the materials used to create the experiment were the same as detailed for Experiment 1. Throughout Experiment 2, four wind-turbines served as landmarks, each of which faced towards the centre of the arena. The landmarks were arranged in a square array, with each 10 m apart. In Stages 1 and 2, four different-sized square boundaries were used (see procedure) instead of the c-shaped wall of Experiment 1. From smallest to largest, the walls that were used to construct the squares were 24 m, 36 m, 48 m, and 60 m. The centre of each square arena was located in the centre of the floor. Each environment was lit by a light source placed 18 m above the centre of the floor, and there were also light sources placed 2 m away from each wall at the corners of the square boundary when it was presented.

During compound training in Stage 3, the smallest square arena was used, and the landmark array was centred to the centre-point of the floor. In these trials, the boundary-related goal was equidistant from the north-east landmark and the intersect of the two walls forming the north-east corner of the square, located halfway along a notional line connecting the landmark and the corner. In Stages 1 and 2 trials the boundary-related goal maintained the same vector from the north-east corner of the boundary as in Stage 3. Returning to the compound arena, the landmark-related goal was located equidistant from the south-west and north-west landmarks, and the centre of the west wall of the square. On trials in which the boundary was larger, or the landmark array was not aligned with the centre of the floor, the goal remained the same distance and direction from the south-west and north-west landmarks.

3.1.3. Procedure

Unless otherwise stated, the details of the procedure for Experiment 2 were the same as those for Experiment 1. During Stages 1 and 2 training for the Landmark Stable group, the array of landmarks remained centred on the centre-point of the floor. For this group, the boundary was made unstable by changing it between four different sizes between trials (see Fig. 4). For the Boundary Stable group, Stage 1 and 2 training was always conducted within the smallest square arena. For this group, the landmark array was made unstable by moving it to one of four positions within the bounded environment. One position was with the centre of the array aligned with the centre of the floor. From here, three further positions were generated by shifting the centre of the landmark array from the centre of the floor along the x,y axes in the following distances: −1.76 m, −2.68 m; 1.76 m, 2.39 m; 1.46 m, 1.26 m. In keeping with Experiment 1, the location of the goal was indicated to participants throughout Stage 1 training, but only indicated to participants if 60s of a given Stage 2 trial elapsed.

Training trials began from one of four locations. In the smallest square arena, three start positions were from the centre of north, east, and south walls. As the centre of the west wall of the small arena was very close to the landmark-related goal, the fourth starting position was the south-west corner. The starting positions remained unchanged, regardless of the size of the boundary or the position of the landmark array on a given trial.

In Stage 3 compound training, both groups received training conducted in the smallest square environment, with the centre of the landmark array aligned with the centre point of the floor. In keeping with Experiment 1, participants in both groups began one trial from each of the four different start locations and both goals were again equidistant

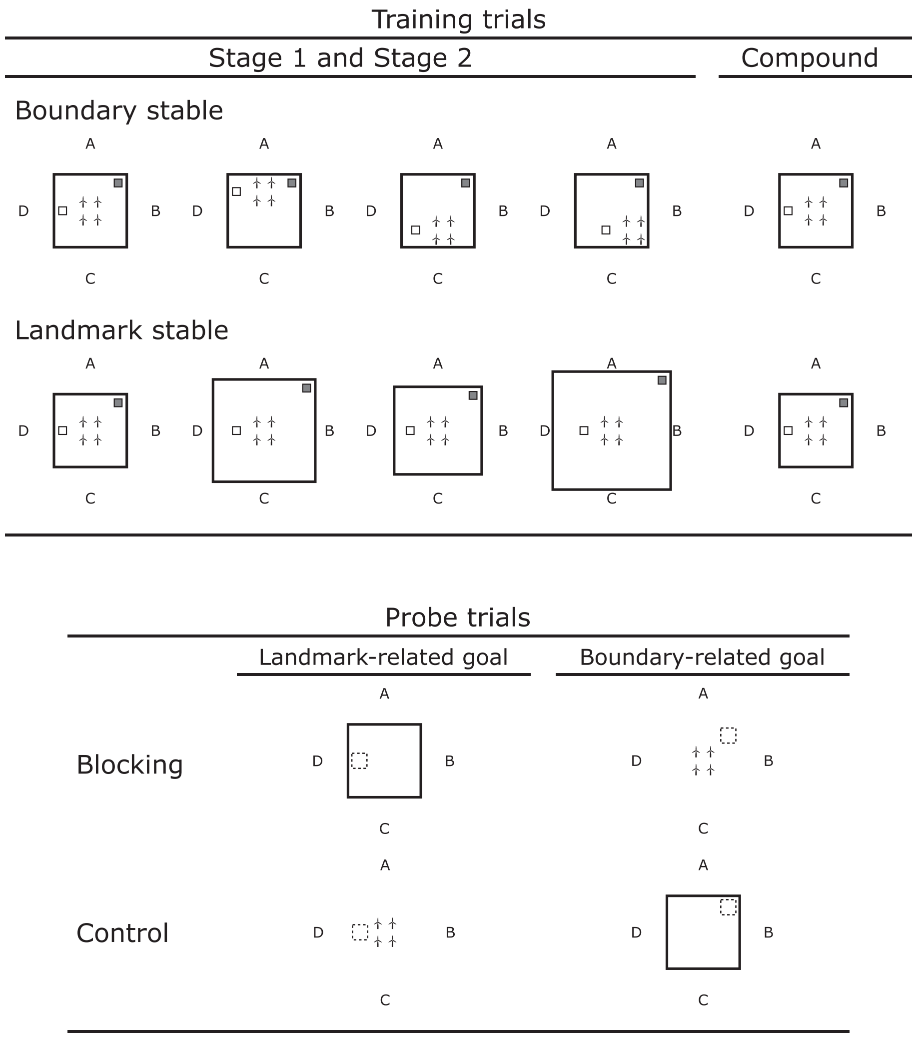

Fig. 4. An example of the trials given to the Boundary Stable and Landmark Stable groups during Stages 1–3 (upper panel) and in Probe trials (lower panel) for Experiment 2. The boundary-related goal is shown as a grey square, and the landmark-related goal as an open square. The distal orientation cues are lettered. During the Probe trials the goals were removed and time spent searching in the goal zones, shown as dotted squares, was recorded.

from the boundary wall and the landmark cues.

Having completed training, participants received 4 unrewarded probe trials that were administered in the same manner as described in Experiment 1, save for the start location. On each probe of Experiment 2, participants began in a novel position near the south-east corner, at a location equidistant from the locations of the boundary- and landmark-related goals during training.

3.2. Results

3.2.1. Stage 1

The left side of the top panel of Fig. 5 shows the mean latencies to find the boundary- and landmark-related goals for both the Boundary Stable and Landmark Stable groups when the goals were visible, similar to the results of the equivalent Stage 1 training in Experiment 1. As in Experiment 1, there were no significant differences between groups in the time taken to locate either the boundary-related goal, $t(30) = 1.63$, $p = .11$, Cohen's $d = 0.58$ [−0.14–1.23], or the landmark-related goal, $t(30) = 1.66$, $p = .11$, Cohen's $d = 0.58$[−0.13–1.29],

3.2.2. Stage 2

The middle of the top panel of Fig. 5 shows the mean latencies to find the boundary- and landmark-related goals for both groups when the goals became invisible. In navigating to the boundary goal, there appears to be little difference between the groups. A two-way (group x block) ANOVA of individual latencies to find the boundary-related goal revealed a significant effect of block, $F(2, 60) = 28.38$, $p < .001$, $\eta_p^2 = 0.49$ [0.32–0.59], but no effect of group, $F < 1$, and no group x block interaction, $F(2, 60) = 2.92$, $p = .07$, $\eta_p^2 = 0.09$ [0.00–0.20]. The equivalent analysis for the landmark-related goal also showed a main effect of block, $F(2, 60) = 12.33$, $p < .001$, $\eta_p^2 = 0.29$ [0.13–0.41], and no overall difference between the groups, $F(1,30) = 3.38$, $p = .08$, $\eta_p^2 = 0.1$ [0.00–0.28], though there was a significant interaction between the main effects, $F(2, 60) = 3.56$, $p = .037$, $\eta_p^2 = 0.11$ [0.004–0.22]. Simple main effects revealed a significant effect of block for the Boundary Stable group, $F(2, 29) = 11.44$, $p < .001$, $\eta_p^2 = 0.44$ [0.18–0.58], but not for the Landmark Stable group, $F(2, 29) = 1.39$, $p = .27$, $\eta_p^2 = 0.09$ [0.00–0.23]. This effect is reflected in the finding that the time to find the goal in the first block was higher for the Boundary Stable than the

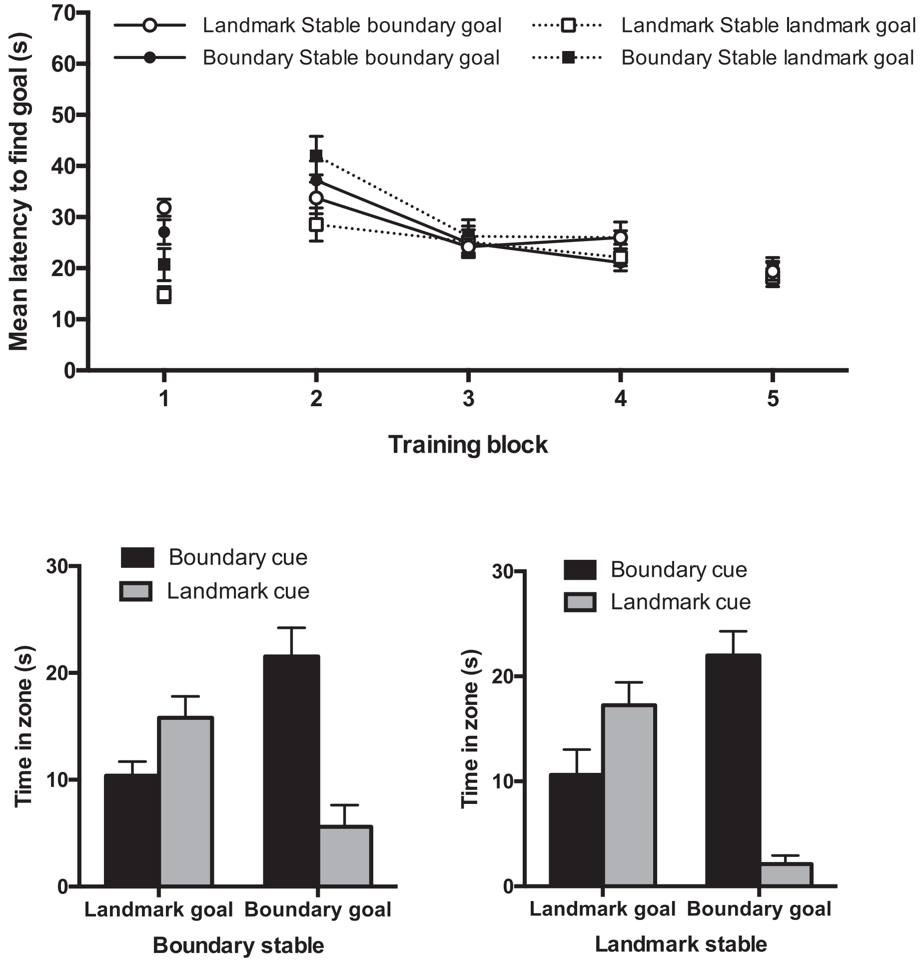

Fig. 5. Upper panel: Mean latencies (± one standard error) for both Boundary Stable and Landmark Stable groups to find the goal during training in Experiment 2. Data are shown in four-trial blocks. Block 1 corresponds to stage 1 training in which the goals were visible. Blocks 2–4 correspond to stage 2, and block 5 to stage 3. Lower panel: The mean percentages of time (± one standard error) spent in the search zones for the Boundary Stable (left) and Landmark Stable (right) groups during the Probe trials of Experiment 2.

Landmark Stable group, $F(1, 30) = 7.37, p = .01, \eta_p^2 = 0.20$ [0.03–0.38], but not in the remaining blocks, $Fs\ (1, 30) < 1.22, ps > 0.28, \eta_p^2 s < 0.04$ [0.00–0.19].

3.2.3. Stage 3

The right side of the top panel of Fig. 5 shows the time to find each goal for each group during compound training. There were no differences between the groups in times taken to locate either the boundary-related goal, $t(30) = 0.06, p = .95$, Cohen's $d = 0.02$–0.67–0.72], or the landmark-related goal, $t(30) = 0.62, p = .54$, Cohen's $d = 0.22$ [−0.48–0.91].

3.2.4. Probes

The bottom panel of Fig. 5 shows the mean time that participants in each group spent searching within the zone surrounding the goal location during tests of learning based on the cues that were predictive of each goal location only from the beginning of the compound Stage (blocking tests) and of learning based on the cues that were predictive throughout training (control tests). Similar to the results of Experiment 1, when searching for the boundary goal, participants in both groups spent more time in the goal zone on control tests relative to blocking tests. This was also true when participants were searching for the landmark goal. However, the difference between the control and blocking tests appeared attenuated in both groups. Two-way ANOVAs of individual time spent in the goal zone, with within-subjects variables of goal (landmark-related or boundary-related) and test cue (landmark or boundary) for both the Boundary Stable and Landmark Stable groups showed interactions between the main effects in both analyses, $Fs\ (1, 15) > 27.39, ps < 0.001, \eta_p^2 s > 0.65$[0.33–0.76]. There was no effect of goal in either analysis, $Fs\ (1, 15) < 1.21, ps > 0.2, \eta_p^2 s < 0.07$ [0.00–0.31], but the main effect of cue was significant in both analyses, $Fs\ (1, 15) > 9.83, ps < 0.01, \eta_p^2 s > 0.40$ [0.08–0.59]. Analysis of simple main effects showed that the time spent in the goal zones in the control tests was greater than that spent in the same zone during blocking tests for both groups regardless of cue type and cue stability during training, $Fs\ (1, 15) > 5.50, ps < 0.05, \eta_p^2 s > 0.27$[0.01.-50].

3.3. Discussion

In keeping with Experiment 1, during probe trials to assess memory for the location of a landmark- and boundary-related goal, participants in both the Boundary Stable and Landmark Stable groups spent more time searching in the goal zone during the control probe compared to the blocking probe. Despite the change in design, aimed at ensuring participants had to use a configuration of proximal (boundary or landmark) and orientation cues to locate the goal, the results did not reveal an immunity to cue competition for either the boundary cues (cue type hypothesis) or the stable cues (cue stability hypothesis). However, despite observing this reciprocal blocking effect, our analysis did reveal that the magnitude of the blocking effect of landmarks by boundaries was greater than the blocking effect that was observed for boundaries by landmarks, regardless of the stability of the cue. This result, which is at least reminiscent of the failure for landmark to block boundary in Doeller and Burgess (2008), raises the possibility that requiring participants to use the distal orienting cues when coding locations relative to the boundary may have played some role in the asymmetric blocking effect reported by Doeller and Burgess (2008).

However, it is possible that these differences in the observed blocking effect are actually the result of a confounding factor in our design. Because of the complexity of the counterbalancing required for the experiments we have described so far, we did not train any subgroups of participants to locate a boundary-related goal in the same location as that used for the landmark-related goal, nor did we perform the reciprocal training, with the landmark-related goal in the same location as that used for the boundary-related goal. Thus, it is possible that there is an unconditioned difference in how easily landmark and boundary cues can be used to code different spatial locations in our task. For example, the boundary-related goal was always near the north-east corner of the square arena, while the landmark-related goal was midway along the westward arena wall in the compound stage. If using the boundary to learn a position midway along a wall is harder than using the same cue to learn a position in one of its corners, because of the difficulty in learning vectors from a corner versus a continuous wall (See Introduction to Experiment 1; Mou & Zhou, 2013), then there may be a difference between blocking and control probes that has little to do with cue competition effects. To rule out this possibility, we conducted Experiment 3 to ensure that differences in cue control for different goal locations could not explain the magnitude of the blocking effects from Experiment 2.

4. Experiment 3

The purpose of Experiment 3 was to assess if there were unconditioned differences in the extent to which the landmark and boundary cues controlled navigation behaviour when the goal was located in the different positions in experimental arena. Group BNE-LW was trained to locate a goal in the north-east corner of a square boundary arena, and another goal to the west of the landmark array, as in experiment 2. The other group, Group BW-LNE, was trained to find a goal to the north-east of the landmark array, and the other to the west of the square boundary. Probe trials were used to assess participants' navigational behaviour following training. If there were no unconditioned differences in the extent to which the square boundary or landmark array could be used to code spatially different goal locations, then we would expect no differences in search preference between the BNE-LW and BW-LNE groups.

4.1. Method

4.1.1. Participants

32 participants (17 female) from Durham University took part in the experiment, and were given course credit in return. Participant ages ranged between 19 and 30 ($M = 20.69$, $SD = 1.96$).

4.1.2. Materials

The materials used to create the experiment were the same as for Experiment 2. The square arena was constructed from 24m walls, and so was the same arena used for the test stages of Experiment 2. Likewise, the landmark array was also identical to that used in the test stages of Experiment 2.

4.1.3. Procedure

The procedural details were the same as for Experiment 2, unless otherwise stated. Participants were trained to locate a goal relative to the boundary or landmark array, with the order counterbalanced between groups. Participants in the BNE-LW group were trained to find one goal that located a fixed distance and direction from the north-east corner of the square boundary, and another located equidistant from the north-west and south-west landmarks of the landmark array. For participants in the BW-LNE group, one goal was located midway along the west boundary wall of the square, and the other goal to the north-east of the landmark array. For each goal there were 4 training trials before a 60s probe trial in the same environment. The goal positions were identical to the landmark- and boundary-related goals in the compound stage of training in Experiment 2, which allowed us to assess whether differences in cue control for different goal locations could explain the magnitude of the blocking effects reported in Experiment 2.

4.2. Results

4.2.1. Training

The mean latencies to locate the north-east goal using the boundary (group BNE-LW) or the landmarks (group BW-LNE) are shown in the upper left panel of Fig. 6. The equivalent data for the west goal using the boundary (group BW-LNE) or landmarks (group BNE-LW) are shown in the upper right panel. Latencies decreased over trials, and there were few differences between the groups. Two-way ANOVAs of individual mean latencies to find the NE or W goals reflected these observations, with both indicating a main effect of trial, $Fs\ (3, 90) > 50.93$, $ps < 0.001$, $\eta_p^2s > 0.63$ [0.51–0.69]. For the NE goal there was a main effect of group, $F\ (1, 30) = 7.67$, $p = .01$, $\eta_p^2 = 0.20$ [0.03–0.39], with the overall time taken to find the goal using the landmark array longer than using the boundary. However, there was no effect of group when finding the W goal, $F\ (1, 30) = 1.49$, $p = .23$, $\eta_p^2 = 0.05$ [0.00–0.21], and no interaction between the main effects for either analysis, $Fs < 1$.

4.2.2. Probes

The results of the test trials are shown in the lower panel of Fig. 6. Participants were able to learn the position of the goal when learning with reference to the boundary regardless of its location. However, it appeared that when learning with reference to the landmarks, participants spent less time searching in the goal zone in the west position compared with when it was in the north-east. A two-way ANOVA of individual time spent in the search zones, with Group (BNE-LW or BW-LNE) as the between-subjects variable and test (Boundary or Landmark) as the within-subjects variable showed a main effect of test, $F\ (1, 30) = 11.71$, $p = .002$, $\eta_p^2 = 0.28$ [0.07–0.46], and a significant interaction between the main effects, $F\ (1, 30) = 18.14$, $p < .001$, $\eta_p^2 = 0.38$ [0.15–0.54], but no effect of group $F\ (1, 30) = 2.09$, $p = .16$, $\eta_p^2 = 0.07$ [0.00–0.23]. Analysis of simple main effects confirmed the observations above, with a significant difference between groups when searching for the west goal (group BNE-LW using the landmarks, and group BW-LNE using the boundary), $F\ (1, 30) = 14.76$, $p = .001$, $\eta_p^2 = 0.33$[0.11–0.50], but no difference when searching for the north-east goal (group BNE-LW using the boundary and BW-LNE using the landmarks), $F\ (1, 30) = 2.02$, $p = .17$, $\eta_p^2 = 0.06$ [0.00–0.23].

4.3. Discussion

The time spent searching for the west goal using the landmarks in the current experiment ($M = 16.5$) was very similar to that in Experiment 2 (Boundary Stable, $M = 15.8$, Landmark Stable, $M = 17.3$). In contrast, when using the boundary to find the same goal participants spent significantly more time than when using the landmarks ($M = 22.3$). The results rule out the possibility that the apparent weak blocking of boundary learning by landmarks, compared with strong blocking of landmark learning by boundary, in Experiment 2, was the result of inherent differences in the ability of participants to code certain locations with reference to boundary and landmark cues in our experimental environment. If that had been the case then we would have expected that participants spent less time searching for the west goal with reference to the boundary than when using the landmarks, when in fact we found the opposite. Equally, the large blocking effect of boundary learning on subsequent landmark learning cannot be explained by difficulty in learning the north-east location with respect to landmarks, because participants in Group BW-LNE learned with reference to the landmarks as well as those in Group BNE-LW learned with reference to the boundary. These results are reassuring, as is the fact that participants had only four trials to learn the locations of the goals relative to the boundary and landmark cues, which was the same as during the compound stage of training in Experiments 1 and 2. Although 4-trial

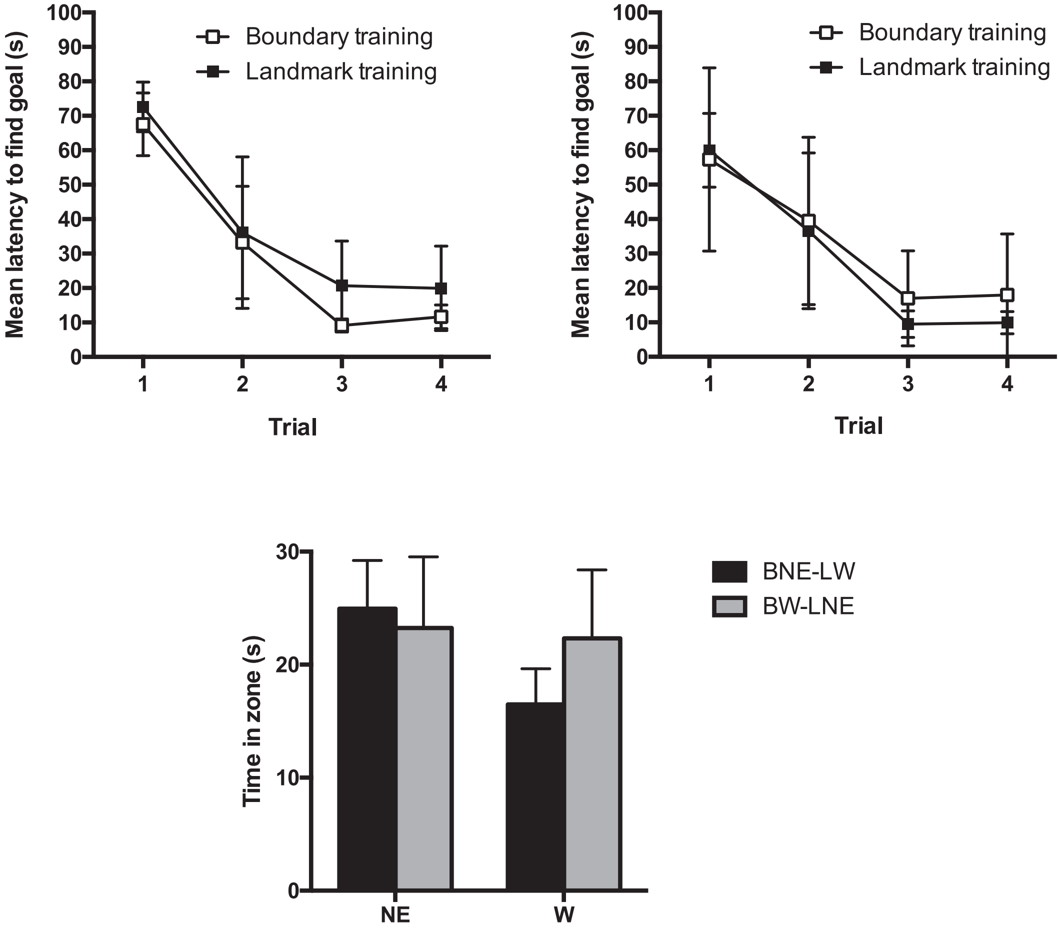

Fig. 6. Upper panel: Mean latencies (± one standard error) to find the north-east goal (left panel) and west goal (right panel) for both groups during training trial in Experiment 3. Group BNE-LW was trained to locate the north-east goal with the boundary cues, and the west goal with the landmarks, while Group BW-LNE was trained to locate the north-east goal with the landmarks and the west goal with the boundary cues. Lower panel: The mean percentages of time (± one standard error) spent in the north-east and west search zones for each group during the Probe trials of Experiment 3.

compound stages have been used in previous spatial studies (e.g. Buckley, Smith, & Haselgrove, 2016b), the fact that search times in the current experiment are comparable to those in the equivalent conditions in Experiments 1 and 2 provides evidence that it is unlikely that the blocking effects observed were a result of too little training in the compound stage.

We can therefore be confident that the blocking effects observed in Experiments 1 and 2 are not due to some simpler explanation relating to limited training or to difficulty in coding some locations. In fact, the apparent weaker blocking of the boundary by the landmarks may be due to the choice in Experiment 2 to the west position of the landmark-related goal, which the current experiment shows is learned less well in relation to the landmarks than the boundary. If learning the landmark-related goal with respect to landmarks was incomplete by the end of stage 2 training in Experiment 2 then there may have been sufficient prediction error for learning to the boundary to progress, resulting in the asymmetrical (but still significant) effect shown in Fig. 5. The results of Experiment 3 thus strengthen the interpretation that the reciprocal blocking effect demonstrated in Experiment 2 is not consistent with either the cue-stability or cue-type hypotheses as set out in the Introduction. In particular, both hypotheses hinge on the notion of dual process, with true spatial learning, based either on an allocentric representation formed from the perception of cue stability (O'Keefe & Nadel, 1978) or from a unique spatial representation based on the use of environmental boundaries (Doeller & Burgess, 2008), utilising a distinct learning mechanism, unconnected to an error-correcting rule such as those thought to underlie associative or reinforcement learning (e.g., Rescorla & Wagner, 1972; Sutton & Barto, 1998).

Cue competition is an effective way of testing the algorithm controlling learning, but the unique paradigm of a navigational task may offer an alternative test of the extent to which cues interact in learning. To further test whether landmarks and boundaries interact in a fashion expected by associative learning we asked whether these different cue types can become associated together, and not just whether they can be shown to be in competition with one another. This would provide a powerful test of the hypothesis that landmarks and boundaries are learned in separable memory systems. Testing this question was the purpose of the final experiment.

5. Experiment 4

To assess if learning in the hypothesised landmark system can become associated with learning in the boundary system, against the predictions of the cue type hypothesis, a goal that had previously been established as being in one location with respect to the boundary was subsequently trained to a new location with respect to the landmark array. At the end of this training, a test trial in the presence of the boundary cues was conducted to determine if the new learning with the landmark array affected participants' search behaviour. Should the goal location with respect to the landmark system be learned independently of the boundary system then the intervening training in the presence of the landmark array should have had no effect on behaviour in the presence of the boundary. Such an approach has been adopted successfully in the rodent literature to account for potentiation of geometry learning by environmental features (e.g., Austen, Kosaki, & McGregor, 2013; Austen & McGregor, 2014; Horne & Pearce, 2009; Rhodes, Creighton, Killcross, Good, & Honey, 2009), but to our knowledge has not been reported in humans.

Participants in all groups of Experiment 4 underwent the same initial and compound training as the Landmark Stable group of Experiment 2. This training first established that one goal location was related to the boundary and the other to the landmark array (Stages 1 and 2) before giving participants the opportunity to learn both goal locations based on both the boundary and landmark cues (compound training). In a subsequent stage, participants underwent reversal training for one of the goal locations in the presence of the landmark cues. As both the square boundary and square landmark array were rotationally ambiguous, the distal cues, presented at infinity, provided orienting information for both cue types. Two groups underwent spatial reversal training in the presence of only the landmark array for one of the two goal locations they had already learned about. For the Boundary goal-reversal group the goal that had been in a consistent location with reference to the boundary in Stage 1 training was moved to the diametrically opposite location in the presence of the landmark array, and the participant was required to learn this new location with reference to the landmark array. For the Landmark goal-reversal group the landmark goal from Stage 1 was moved to the opposite location, and, similar to the previous group, training continued in the presence of the landmark array. As a control, the third group in the experiment continued to receive training in which both goal locations were in the same locations as during compound training. However, as was the case for the experimental groups, only the landmark and distal orientation cues were present. The inclusion of this group was crucial to ensure that the reversal training affected navigation only to the goal that had been moved, and did not disrupt all navigation behaviour. Following the reversal training stage, participants received two probe trials conducted in a square arena that was oriented by the four distal cues, and we measured the time that participants spent searching in zones that surrounded the originally trained and reversed locations.

If learning with respect to boundary information occurs within an encapsulated system that is immune to interference from landmark learning, then the reversal training in the presence of the landmark array for the two experimental groups should not affect performance based on the boundary cues when they are re-presented at test. Consequently, the cue-type hypothesis anticipates the reversal stage in the current experiment to have no effect on how participants subsequently navigate using boundary cues. At test, therefore, performance in both the Boundary goal-reversal and Landmark goal-reversal groups should be equivalent to the Control group. Alternatively, consistent with the blocking effects detected in Experiments 1 and 2, non-modular domain-general associative accounts would assume that learning based on one set of cues has the potential to affect performance based on another. For the boundary goal probe, therefore, this domain-general hypothesis predicts that participants in the Control and Landmark goal-reversal groups will show a strong and equal preference for searching in the trained over the reversed location, but that this effect will be attenuated in the Boundary goal-reversal group. Similarly, for the landmark goal probe, participants in the Control and Boundary goal-reversal groups should show a strong and equal preference for searching in the trained over the reversed location, but this effect should be attenuated in the Landmark goal-reversal group.

5.1. Method

5.1.1. Participants

48 participants (19 female) from Durham University took part in the experiment, and were given course credit in return. Participant ages ranged between 18 and 22 ($M = 20.19$, $SD = 1.00$).

5.1.2. Materials

All materials were identical to those described for Experiment 2.

5.1.3. Procedure

For all three groups of the experiment, the procedure of Stage 1, Stage 2, and Stage 3 training, was identical to that described for the Landmark Stable group of Experiment 2.

The groups in the current experiment were differentiated by the reversal treatment that they received in Stage 4. During the 8 trials of Stage 4, the centre of the landmark array was aligned with the centre of the floor, and participants navigated in the absence of the boundary wall, but with the four orientation cues present. On trials in which participants in the Boundary goal-reversal group were required to locate the boundary goal, it was now located near to the SW landmark in the array, having previously been located by the NE landmark in the array during compound training. On trials in which Landmark goal-reversal group were required to locate the landmark goal, it was now located between the NE and SE landmarks of the array, having previous been located between the NW and SW landmarks of the array in compound training. In short, during the reversal preparation a goal that moved was now located in the diametrically opposite part of the landmark array. For the Control group, neither the landmark- or boundary-goal moved for the trials administered in Stage 4 training (see Fig. 7). During each block of 4 trials, participants began once from each start location, and again trials were pseudo-randomised such that participants were not required to locate the boundary- or landmark goal on more than two consecutive trials.

Following reversal training, participants received two probe trials, in which they were allowed to navigate within the square arena for 60s. For one probe trial they were cued to search for the landmark goal, and in the other they were cued to search for the boundary goal. The order of these trials was counterbalanced across participants in each group. To assess performance, we measured the time participants spent searching in two square search zones, with side lengths double that of the goal (4.28 m). The centre of one search zone was aligned with the centre of the goal location during compound training (named here the ‘trained’ zone), whilst the centre of the other search zone was aligned with the centre of the goal location during reversal training (named here the ‘reversed’ zone), which took place in the absence of the boundary cues. As with Experiment 2, participants began each of these probe trials near the south-east corner of the square.

5.2. Results

5.2.1. Stage 1

Fig. 8 shows the mean latencies to find the boundary- (upper panel) and landmark- (lower panel) goals for each group when the goals were visible. One-way ANOVAs of individual mean times to find each goal unsurprisingly revealed little difference among the groups, *Fs* $(2, 45) < 1.60$, *ps* > 0.2, η_p^2s < 0.07 [0.00–0.18].

5.2.2. Stage 2

During this stage, in which the goals were first made invisible, the times to find each goal reduced over training. Two-way Group x block ANOVAs of individual mean latencies revealed main effects of block for both boundary and landmark goals, *Fs* $(2, 90) > 14.89$, *ps* < 0.001, η_p^2s > 0.25 [0.12–0.35], but no effect of group, *Fs* $(2, 45) < 1.40$, *ps* > 0.26, η_p^2s < 0.06 [0.00–0.17], and no interactions between the main effects, *Fs* $(4, 90) < 1.31$, *ps* > 0.27, η_p^2s < 0.06 [0.00–0.11].

5.2.3. Stage 3

In this stage, in which the landmarks and boundary became stable with respect to one another, there were few differences between the groups. One-way ANOVAs of individual mean times to find each goal revealed no differences among the groups, *Fs* $(2, 45) < 1.41$, *ps* > 0.25, η_p^2s < 0.06 [0.00–0.17].

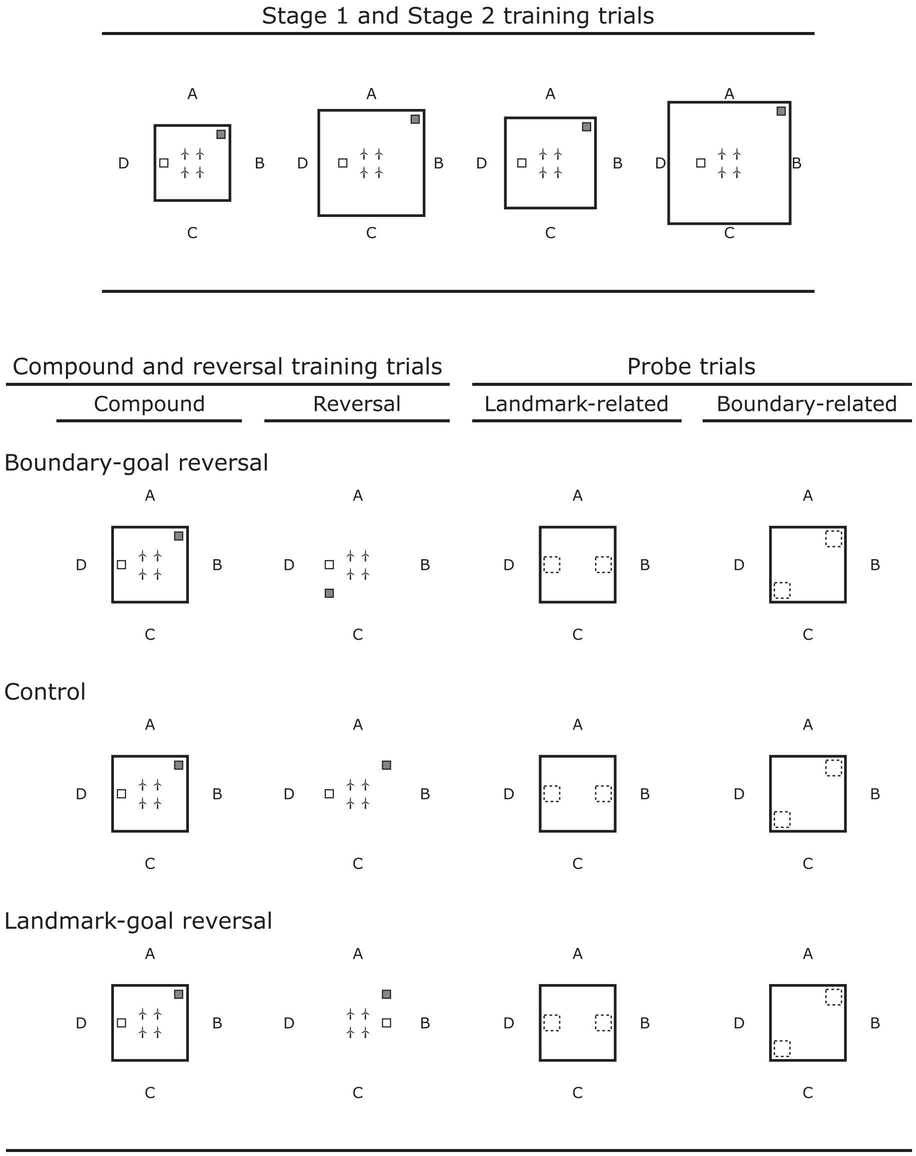

Fig. 7. An example of the trials given to all groups during Stages 1 and 2 (upper panel) and in Stages 3 and 4 and Probe trials (lower panel) for Experiment 4. The boundary-related goal is shown as a grey square, and the landmark-related goal as an open square. The distal orientation cues are lettered. During the Probe trials the goals were removed and time spent searching in the goal zones, shown as dotted squares, was recorded.

5.2.4. *Stage 4*

The right side of each panel of Fig. 8 shows the mean latencies to find the boundary and landmark goals for each group during the reversal stage of the experiment. For both boundary (upper panel) and landmark (lower panel) goals, the latencies for the reversal group (Boundary goal-reversal for the boundary goal and Landmark goal-reversal for the landmark goal) were noticeably longer, particularly in block 1, than for the non-reversal group (Landmark goal-reversal for the boundary goal and Boundary goal-reversal for the landmark goal) or the Control group. Two-way Group x block ANOVAs of individual mean latencies to find each goal both showed significant effects of Group, *Fs* (2, 45) > 8.48, *ps* < 0.001, η_p^2s > 0.27 [0.09–0.41], block, *Fs* (2, 45) > 4.32 *ps* < 0.05, η_p^2s > 0.16 [0.02–0.30], and interactions between the main effects, *Fs* (2, 45) > 6.20, *ps* > 0.01, η_p^2s > 0.22 [0.05–0.36]. Analyses of simple main effects for each interaction showed a significant difference among the groups in block 1, *Fs* (2, 45) > 7.37, *ps* < 0.005, η_p^2s > 0.25 [0.07–0.39], though there was no difference among the groups in block 2, *Fs* (2, 45) < 1.77, *ps* > 0.18, η_p^2s < 0.07 [0.00–0.19]. Pairwise comparisons of differences among groups for block 1 of the boundary goal latencies showed the Boundary goal-reversal group latencies were longer than both the Landmark goal-reversal group and the Control group, as observed above. However, there was no significant difference between the Landmark goal-reversal group and the Control group. Similarly, pairwise comparisons of differences among groups for block 1 of the landmark goal latencies showed that Landmark goal-reversal latencies were longer than Boundary goal-reversal or Control latencies, but there was no difference between Boundary-goal reversal and Control latencies.

5.2.5. *Probes*

To analyse probe data, difference scores were calculated for each participant, whereby the time spent searching in the reversed zone on a given test was subtracted from the time spent searching in the trained zone on the same test. This was possible in the current experiment, but

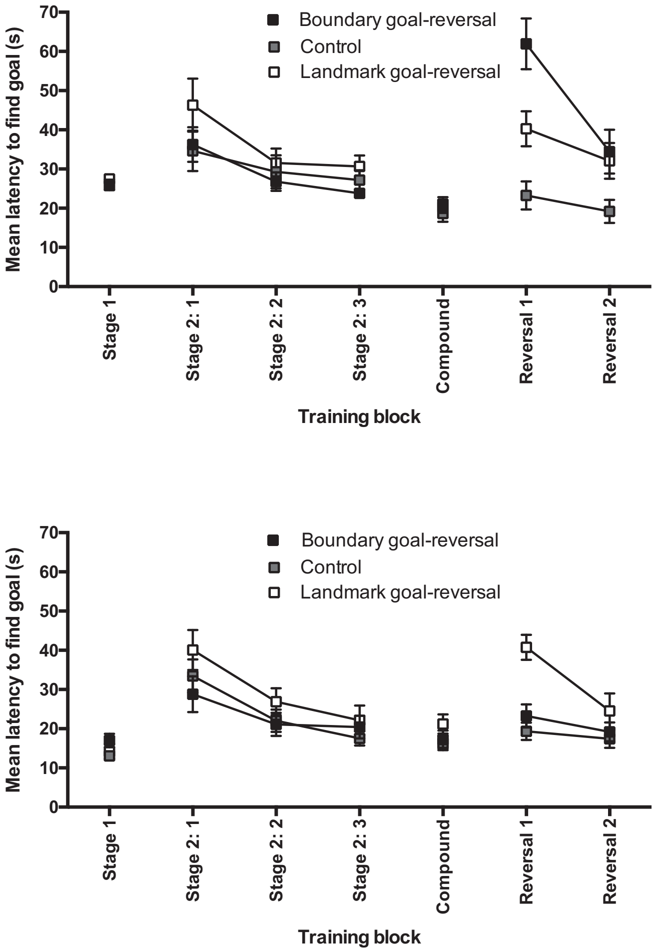

Fig. 8. Mean latencies (± one standard error) to find the boundary goal (upper panel) and landmark goal (lower panel) for the Boundary goal-reversal, Landmark goal-reversal, and Control groups during training in Experiment 4. Data are shown in four-trial blocks. Block 1 corresponds to Stage 1 training in which the goals were visible. Blocks 2–4 correspond to stage 2, and block 5 to stage 3. Blocks 6 and 7 correspond to the reversal stage.

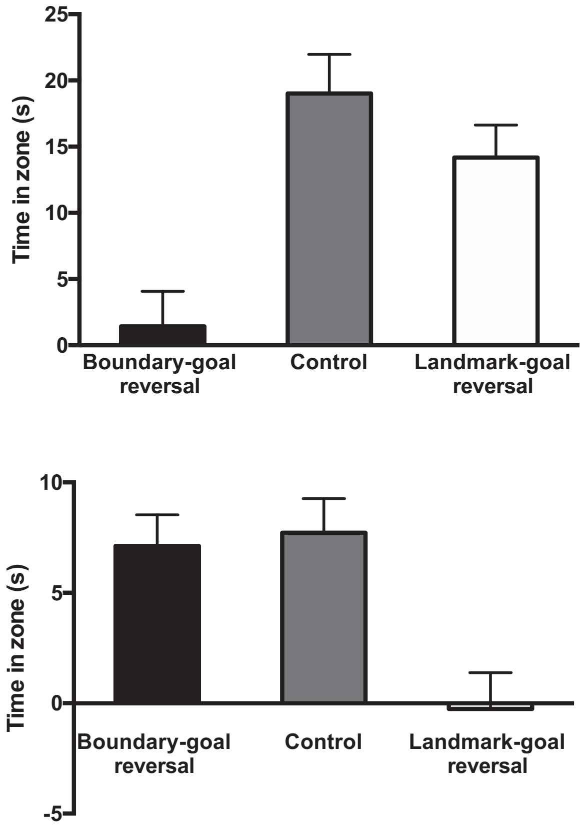

Fig. 9. The mean difference scores (± one standard error) for each group during the Boundary-goal Probe trial (upper panel) and Landmark-goal Probe trial (lower panel) of Experiment 4.

not Experiments 1 and 2, because the zone data here were collected within the same probe trial. Positive scores represented a preference for searching at the originally trained location, negative scores represented a preference for the reversed location, and scores close to zero represent no preference for either location. The top panel of Fig. 9 shows the difference scores for each group during the boundary goal probe, while the bottom panel shows the same groups in the landmark goal probe. In both probes the reversal group showed little preference for the goal location that was associated with the boundary during training, while the non-reversal and control groups did.

One-way ANOVAs conducted on individual difference scores from both the boundary and landmark goal probes revealed significant effects of group, Fs (2, 45) $>$ 8.39, MSEs $>$ 37.75, ps $<$ 0.001, η_p^2 s $>$ 0.27 [0.08–0.41]. For both analyses, pairwise comparisons showed that the reversal group (Boundary goal-reversal for the boundary goal probe and Landmark goal-reversal for the landmark goal probe) showed a significantly weaker preference for the boundary-associated location than either the non-reversal groups (Landmark goal-reversal for the boundary goal probe and Boundary goal-reversal for the landmark goal probe) or the Control group, and that there was no difference between the non-reversal and control groups. Furthermore, one sample t-tests revealed that in the boundary goal probe Boundary goal-reversal difference score did not differ from chance, t (15) = 0.54, p = .59, d = 0.14, while those for the other two groups did, ts (15) $>$ 5.77, ps $<$ 0.001, d $>$ 1.44. Conversely, in the landmark goal probe, the Landmark goal-reversal difference score did not differ from chance, t (15) = 0.16, p = .88, d = 0.04, while those for the other two groups did, ts (15) $>$ 5.01, ps $<$ 0.001, d = 1.25.

5.3. Discussion

During the boundary goal probe, participants in the Landmark goal-reversal and Control groups displayed a significant preference for the trained location. In contrast, the Boundary goal-reversal group displayed no preference for either zone. For the landmark goal probe, participants in the Boundary goal-reversal and Control groups displayed a significant preference for the trained location, but those in the Landmark goal-reversal group displayed no preference for either zone. Together, these results indicate that revaluing a goal location with respect to the landmark array affects subsequent behaviour in a test trial conducted with a boundary. These results are not consistent with theories that suggest learning about boundary information is a modular process that occurs without interference from landmark cues (Doeller & Burgess, 2008: see also Cheng, 1986; Gallistel, 1990), but are expected by assuming that learning based on landmark cues are capable of influencing behaviour controlled by boundary cues in a manner consistent with a domain-general associative account.

The results of Experiment 4 are consistent with a hypothesis that attenuated blocking (Experiment 2), or even the absence of blocking (Doeller & Burgess, 2008), could be due to generalisation of spatial search from one cue type to the other because of the presence of orientation cues that are common to both environments. In Experiment 4, by moving a goal with respect to one cue type (landmarks – and by extension also the orientation cues), participants altered their spatial search in the presence of the other cue (a boundary sharing the same orientation cues). This demonstration, in a procedure unrelated to cue competition, extends the generality of our findings from Experiments 1 and 2. Importantly, because no incidental learning mechanism is assumed to be necessary for such an effect, it reduces the possibility that those previous demonstrations of weaker or absent blocking of boundaries by landmarks is attributable to incidental learning.

6. General discussion

The experiments reported here were designed to test the circumstances under which spatial learning is under the control of distinct learning algorithms. It was hypothesised that spatial learning would be under the control of a domain general error-correcting mechanism if the cues were discrete landmarks, but that locations that could be coded with reference to environmental boundaries would be under the control of an incidental learning rule (cue type hypothesis). Alternatively, the error-correcting mechanism was hypothesised to act when cues in the environment were perceived to be unstable, but that if they were in a stable frame of reference they could be used by the incidental cognitive mapping system (cue stability hypothesis). Despite manipulating both cue stability and cue type, reciprocal blocking was observed, against the predictions of both hypotheses. The reciprocal blocking effects were also obtained irrespective of whether the distal cues were crucial for orientation information (Experiment 2), or whether the landmark and boundary itself contained orienting information (Experiment 1). The blocking effects observed in Experiment 2 were not due to some idiosyncratic difficulty in coding different locations with respect to different cues (Experiment 3). In Experiment 4, reversal of one goal location with reference to landmarks influenced where participants searched for that goal, but not another, that had not undergone reversal training, when navigating with respect to the boundary. The results weaken the notion of a 'geometric module' for place learning, as proposed by Doeller and Burgess (2008), because information within the module (boundaries) should not be influenced by information processed outside (landmarks). Overall, the results of the four experiments presented here are consistent with the notion of all spatial learning being under the control of a single domain general error-correcting mechanism (see also Chamizo, 2003; McGregor, 2020; Miller & Shettleworth, 2007, 2008; Pearce, 2009), as opposed to either of the two cognitive mapping theories (cue type and cue stability) tested here.

While our experiments were designed to test two cognitive mapping theories that could be used to explain the results of Doeller and Burgess (2008), it is necessary to consider how our paradigms differed. The main differences between our experiments were that a) we used a goal-finding task, as opposed to participants indicating the location of a previously collected object, and b) in Experiments 2–4, we used a square array of landmarks, together with a square boundary, as opposed to a single landmark within a circular boundary. Both of these factors may be important, but we believe that they strengthen the interpretability of our results rather than weaken it. We argued in the Introduction to Experiment 1 that a goal-finding task could increase motivation for location learning, thereby maximising the opportunity to detect blocking. This is because in error-correcting theories of learning, blocking is at its maximum when learning with the blocking cue is complete, with low prediction error between what can be learned and what has been learned. With the introduction of a second cue in the compound stage, complete learning to the blocking cue leaves no opportunity for learning to the second cue to occur. Nevertheless, a recent demonstration of overshadowing of boundary learning by a landmark (Zhou & Mou, 2019) in an object-location procedure demonstrates that our results have generality beyond the choice of spatial learning task.

In terms of having a square array of landmarks, and square boundary, this manipulation enabled us to create instability within the environment while also enabling an accurate representation of the boundary-related goal location, as described in the Introduction to Experiment 2. The boundary-related goal could not be learned with reference to the stable landmarks during the initial training stages for the Landmark Stable condition, and yet learning to the boundary still blocked learning about the significance of landmarks when they became relevant in the compound stage, which contradicted the cue stability hypothesis. However, the opposite was also true, with landmarks blocking the boundary, contradicting the cue type hypothesis.

Given the differences between our results and those of Doeller and Burgess (2008), some comment is required. Ours is not the first study to demonstrate that a geometrically unstable cue is capable of blocking subsequent learning about a stable set of cues that might be argued to form the basis of a cognitive map. Redhead, Roberts, Good, and Pearce (1997) demonstrated such an effect in a water maze with rats using a beacon attached to the platform. With the same species, Diez-Chamizo, Sterio, and Mackintosh (1985) varied the positions of featurally discriminable arms in a Y-maze, before fixing them with respect to the stable room cues, demonstrating that the rats' prior experience prevented them from learning the location of food with respect to the positions of the arms within the room. A problem with both of these studies is that the observed blocking effect might have been because in Stage 1 training, the stable room cues were established as unreliable for locating the target (food or platform), and later failure to learn about the newly-relevant room cues in the compound training stage may have been due to animals ignoring them. Another way of putting this is to say that learning about the irrelevance of the room cues in Stage 1 of training caused them to lose associability (Mackintosh, 1973). Doeller and Burgess's (2008) design suffers from a similar flaw in that during stage 1 training either the boundary or landmark was set up to be an unreliable cue, and means that their results may have been due to differences in the extent to which boundary and landmark cues, or stable and unstable cues, are subject to learned irrelevance effects. In contrast, in our experiments, we established the boundary and landmark cues to be equally relevant in Stage 1 training because they each predicted the locations of one of the goals. Thus, the results of the experiments we have reported provide a stronger test of blocking than those of Doeller and Burgess (2008).

Our results with humans are reminiscent of another study with rats (Roberts & Pearce, 1999; see also Biegler & Morris, 1999), which avoided the problem of conflating blocking with reduced associability by training in Stage 1 with curtains drawn around their water maze, thus obscuring the room cues that were to be made available in the compound training stage. However, in their study the beacon that indicated the platform's location was considerably closer to the platform than the stable room cues, thus creating a further conflation – that of the distance of cues to the goal location, which is a strong predictor of their reliability for spatial learning (Bennett, 1993; Cheng, 1990; Kamil & Cheng, 2001). Thus, the beacon may have been perceived as more salient than the room cues in Robert and Pearce's (1999) study. Similarly, in Doeller and Burgess (2008) the locations of objects that were related to the boundary during Stage 1 training were positioned close to the periphery, while landmark-related objects were positioned close to the landmark, which moved around the arena between trials. When the landmark became predictive of the locations of boundary-related objects in the compound stage, the average landmark-object distance was far greater than the average boundary-object distance (Experiment LB, Fig. 3, Doeller & Burgess, 2008). In contrast, because of the placement of the landmark in the compound stage, the average boundary-object distance for landmark-related objects was approximately equal to the average landmark-object distance. Therefore, the effect of this disparity was to make the boundary a reliable cue for landmark-related objects, but made the landmark a poor indicator of boundary-related object location. Such a manipulation would alter the relative salience of the landmark and boundary cues for different objects (see also Cheng, Shettleworth, Huttenlocher, & Rieser, 2007 for discussion in relation to a Bayesian framework for studying spatial learning). In our Experiments 1 and 2, the distance to each goal from the landmark array and boundary was equated during compound training, to ensure that the reliability of each cue type for locating the goal location was equal. Therefore, the cues were both equally predictive during compound training, and yet we still observed cue competition as predicted by associative learning theories.

Under rather different conditions, Zhou and Mou (2016) have also argued against the distinction between boundaries and landmarks as cues that support cognitive maps and associative spatial representations, respectively. While evidence of cognitive mapping in cue competition designs is evidenced by an immunity to interference during learning, Zhou and Mou (2016) argued that a participant's ability to calculate a vector from one object to another that had only been presented sequentially during training should require a cognitive map. Furthermore, if the cue type hypothesis was correct then calculating that vector after coding individual object locations with reference to a circular boundary should be more accurate than coding the object locations with reference to a single landmark. The results showed the opposite effect, which Zhou and Mou (2016) argued was more consistent with a vector addition model than the action of a cognitive map based on boundaries (see also Cheng, 1989; Collett, Cartwright, & Smith, 1986). In this vector addition model, a cognitive map is built from fragments of the environment rather than as a global whole (see also Sawa, Leising, & Blaisdell, 2005). Together, the results presented here and those reported by Zhou and Mou (2016); see also Mou & Zhou, 2013; Zhou & Mou, 2018) are not consistent with the cue type hypothesis, and also weaken the requirement for a boundary-based cognitive map as an explanation of complex flexible spatial behaviour.

We have offered a number of explanations for the difference between our results and those that support a cognitive mapping account based either on cue type or cue stability. More generally, it should be noted that the argument for an incidental learning mechanism depends on the failure to detect the cue competition effects that are a hallmark of error-correcting associative or reinforcement learning models. This places spatial learning theories of this kind (see also Cheng, 1986) in something of a precarious position, because they rely on a null result for support (but see Cheng, 2008). However, there are a number of factors in spatial learning studies that could account for a failure to detect cue competition effects, such as differences in the relative salience of cues (see Buckley, Smith, & Haselgrove, 2014, 2015), the failure to attend to both sets of cues at the same time, or the presence of within-compound associations that effectively counteract any cue competition effect (see, for example, discussion in Pearce, Graham, Good, Jones, & McGregor, 2006; Kosaki, Austen, & McGregor, 2013; Austen et al., 2013). Within the field of associative learning more generally, a recent response by Soto (2018) to a study investigating the replicability of blocking in Pavlovian conditioning in rats (Maes et al., 2016) argued that a number of existing models of associative learning anticipate the parameters that are likely to lead to a failure of blocking (Kinder & Lachnit, 2003; Soto, Gershman, & Niv, 2014; Wagner, 2003), and are able to predict the failures of blocking reported by Maes et al. (2016). Sanderson, Jones, & Austen (2016) recently examined the parameters that promote the detection of blocking in mice, such as cue salience and the extent of phase 1 conditioning, but more systematic studies of this kind are necessary. In relation to studies on incidental spatial learning, there is a clear need for experiments that do not rely on an absence of evidence to support the existence of distinct learning mechanisms, and in particular any claims of incidental learning of cues. Our Experiment 4 may provide a way forward in a way that does not involve cue competition procedures.

More generally, our results raise the question of what is meant by a memory system. There seems no reason to doubt, in the face of overwhelming evidence, that information is learned and stored within separate systems that are predisposed to process specific types of information when faced with the same learning episode (Balleine & Dickinson, 1998; Killcross & Coutureau, 2003; Kosaki, Pearce, & McGregor, 2018; Packard, Hirsch, & White, 1989; Packard & McGaugh, 1996; White, 2008; Yin, Knowlton, & Balleine, 2004). Whether this kind of localisation of function constitutes cognitive modularity of the kind proposed by cognitive mapping theory is, however, an important consideration. Various arguments based around anatomical specificity (e.g., Doeller et al., 2008; Jeffery, 2010) or adaptive specialisation (e.g., Gallistel, 1990; Rozin & Kalat, 1972) have been put forward to support the idea of the independence of memory systems. However, as Sherry and Schacter (1987) have pointed out, it does not necessarily follow that the mechanisms for learning, storing, and remembering specific types of information operate according to different rules, just because different types of information are represented in memory (p. 440). Even if we were to call these different anatomically distinct systems 'modules', their rules of operation may be identical. Sherry and Schacter (1987) argued, instead, that memory systems could only be recognised as such if they were characterized by a fundamental distinction in their rules of operation – that their mechanisms differed. Further, the key to the evolution of these memory systems was the incompatibility of mechanism across systems. Sherry and Schacter (1987) offered some examples of these memory systems, including song learning, spatial memory in food-storing birds, and imprinting. However, under their own definition for memory systems, the domain-specific rules of operation of each of these has been somewhat eroded subsequently (e.g., Bateson, 2000; Bateson & Horn, 1994; Bolhuis, De Vos, & Kruijt, 1990; Bolhuis, 1991; Bolhuis & Macphail, 2001; Macphail & Bolhuis, 2001).

Perhaps a resolution to this debate is available if, as Heyes (2003, 2018) has done, we consider the rules of operation, and the type of information processed, as separate components of how a memory system may operate. In terms of the experiments in the current study, boundaries may be afforded a special status over landmarks during learning not by a different learning mechanism (rule of operation), but by a bias in processing or perception. Heyes (2003) termed such an effect *phylogenetic inflection*, to describe a specialisation of input as opposed to a specialisation of mechanism, which she termed *phylogenetic construction*. Therefore the actual representations, in this case one based on boundaries and one based on landmarks, may be domain-specific in that there is a specialised process for building each representation. But learning about the representations may not follow different rules of operation – that is domain-general. However, this account is quite different from cognitive mapping theory, which claims that the immunity of boundary/stable cue learning to cue competition was evidence of a distinct learning mechanism from learning based on landmarks/unstable cues. An account based on phylogenetic inflection and construction is appealing, however, as it acknowledges the distinction between cue types, whilst still anticipating the cue competition effects observed in our experiments. In this sense, our results are consistent with a multiple memory systems framework that emphasises type of information processed (White & McDonald, 2002). But they are at odds with the notion of separate memory systems that operate in parallel, because the rules of operation for each system seem to be domain-general rather than domain-specific (Heyes, 2003). Indeed, associative competition between spatial memory systems at the level of learning has been demonstrated both by the failure of cognitive mapping when landmark vectors are particularly salient, and by the facilitation of learning governed by one system when the other is lesioned (Kosaki et al., 2015; Poulter et al., 2019; see also Gibson & Shettleworth, 2005). Further research, in addition to the purely behavioural studies we report here, and those of Mou and colleagues discussed above, will be required to test the possibility that functionally distinctive brain systems compete for control over learning.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cognition.2021.104802.

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