Running Head: Cue-Placement Modulates Cue Dominance

The effects of cue placement on the relative dominance of boundaries and landmark arrays in goal localization

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Abstract

Two types of visual features are identified as reference points used by individuals to encode locations: surface-based boundaries and discrete-object-based landmarks. Previous research show that learning locations relative to a boundary can overshadow learning relative to a landmark, but not vice versa, suggesting that environmental boundaries play a privileged role in representing individual locations (Doeller & Burgess, 2008). However, other research has revealed that a less accurate cognitive map is derived from boundary-related learning than from landmark-related learning, suggesting that a boundary is less privileged in representing inter-location spatial relations (Zhou & Mou, 2016). The current study aims to reconcile these inconsistent findings. Experiment 1, using both a cue-competition paradigm and a cognitive mapping task, replicated the finding that participants preferred a circular boundary to a four-landmark array for encoding four locations (1A), but that the cognitive maps of the locations derived from the landmark array were more accurate (1B). Using the cue-competition paradigm, Experiments 2-4 manipulated the placement and distinctiveness of the two cues. The results showed that manipulating the placement of the landmark array effectively modulated the relative reliance upon the boundary/landmark-array in encoding individual location. Whereas increasing the distinctiveness of the landmark-array alone is not sufficient to eliminate the boundary advantage in localization. We propose that the boundary privilege occurs in selecting reference points for encoding locations due to its relative peripheral placement in the environment, whereas the landmark advantage occurs in inferring inter-location spatial relations due to the common reference point provided by the single landmark.

Keywords: Boundary, Cognitive map, Landmark, Cue competition, Localization

Localizing oneself and other places of interest is important in our daily life. Successful navigation relies on accurate representations of individual locations. Various cues drawn from a physical environment (e.g., visual features in the surroundings) and in the course of navigation (e.g., proprioceptive cues generated from locomotion through the environment) support the encodings and representations of individual locations. For the current study, we focused mainly on the visual features available in the environment. The localization literature has identified two major types of environmental visual cues that can serve as reference points for encoding locations (Burgess, 2008; Lew, 2011): surface-based boundary cues (e.g., walls, rivers) or discrete-object-based landmark cues (e.g., buildings, trees).

Differences in the processing of the two cues in a localization task were initially found in lesion studies on rats using Morris Water Maze (MWM) tasks (Morris, 1981). In one typical setup, rats were trained to swim to a submerged platform in a circular water tank filled with opaque water. Distal visual features were provided outside the water tank so that rats could keep oriented, but these orientation cues could not offer information regarding the exact location of the platform. Instead, the platform location could be determined relative to the boundary of the tank (i.e., in certain distance away from a part of the wall; e.g., Morris, 1981; Hamilton, Akers, Weisend & Sutherland, 2007) or relative to an intramaze landmark (i.e., bearing a certain spatial relation relative to an intramaze landmark; e.g., Pearce, Roberts & Good, 1998). Several studies showed that hippocampal lesion in rats resulted in their failure to find the submerged platform when the platform location was fixed in the circular water tank; however, the lesion did not prevent rats from using a beacon cue (e.g., a visual feature attached to the platform) to find the platform (Morris, 1982; Packard & McGaugh, 1992; McDonald & White, 1994). Moreover, the hippocampal lesion did not impair rats' ability to locate a platform that had a fixed spatial vector relative to an intramaze landmark even though the landmark moved within the water maze across trials (Pearce, Roberts & Good, 1998). Given these findings, it has been proposed that learning locations in relation to the extramaze distal cues and the boundary is a form of place learning that relies on the hippocampus, whereas learning locations relative to the intramaze landmark might be hippocampal-independent (Burgess, 2008; see also Bullens et al., 2010).

The proposal that boundary processing in spatial localization relies on the hippocampal systems is further supported by the discovery of place cells within rats' hippocampus (O'Keefe & Dostrovsky, 1971; O'Keefe, 1976); the firing of these cells corresponds to the locations of a rat moving in a given environment. Since the initial discovery of place cells, several models have been put forward to explain how they code spatial information (for review, see Redish, 1999). One of the influential models proposed by O'Keefe and Burgess (1996) postulates that environmental boundaries act as a major input to drive the location-specific firings of hippocampal place cells, based on their finding that a given place cell would reach its peak firing when the rat (moving in a rectangular or square enclosure) was at a fixed distance from an enclosure wall in a fixed allocentric direction (the reference system define by the main axes of the enclosure). A later modified version of the model, the Boundary Vector Cell (BVC) model, suggested that individual place cells received a summation of inputs from an ensemble of boundary vector cells (BVCs) whose firings were thought to be tuned to a barrier or a boundary at a given distance and allocentric direction from a rat (Hartley et al., 2000; Hartley, Trinkler & Burgess, 2004; Barry et al., 2006; Burgess, 2008). The existence of the hypothetical BVCs was also confirmed in the subiculum of rats (Lever et al., 2009). Contrary to the finding that environmental boundary information exerts control over the firing of place cells and the hippocampal systems, landmark arrays placed in the center of a cylinder arena were shown to exert little control over the firing field of place cells

(Cressant, Muller & Poucet, 1997). Interestingly, when the object array was moved to the periphery of the arena, either in a clustered or far-apart configuration, the array exerted strong control over the field position of the hippocampal place cells (Cressant et al., 1997). This observation implies that 1) object-based landmarks could be processed by the hippocampus for spatial coding; 2) the degree of control of an intra-maze landmark array over place fields might be critically dependent on the placement of the array within the maze.

Neuroimaging studies on human participants have also demonstrated that environmental boundaries, in contrast to discrete local landmarks, seem to be a major input driving human hippocampal activations. Using functional MRI to examine the neural bases of participants performing a localization task in a virtual-reality (VR) environment, Doeller, King and Burgess (2008) found that encoding locations relative to a circular boundary corresponded to neural activation in the hippocampus; meanwhile, encoding relative to a single landmark within the boundary was associated with activation in the dorsal striatal area. Another fMRI study demonstrated that imagining horizontal boundaries rather than vertical columns was associated with left hippocampal activation (Bird, Capponi, King, Doeller & Burgess, 2010). On the other hand, there is evidence demonstrating that flexible location coding relative to landmarks also engages the hippocampal system (Wegman, Tyborowska & Janzen, 2014; Save & Poucet, 2000a). In their fMRI study, Wegman and colleagues found that the hippocamps was involved in learning locations based on landmark configurations. Taken together, it seems that there could be multiple systems underlying landmark-related spatial learning, depending on the navigational role of a landmark involved in a given navigation task (Chan, Baumann, Bellgrove & Mattingley, 2012).

The differing effects of the boundary cue and the landmark cue on behavioral localization tasks are also observed in human participants (Doeller & Burgess, 2008). Using a cue-competition paradigm (overshadowing and blocking), Doeller and Burgess examined competition between a landmark cue and a boundary cue in goal localization. In their overshadowing experiment, participants learned to place four objects relative to a featureless circular wall (the boundary condition), a single traffic cone (the landmark condition, with the landmark placed within the radius of the boundary) or with the presence of both cues (the two compound-cue conditions). Distal orientation cues were available in all of the conditions but they provided only the heading information. To precisely locate the four objects, participants had to rely on the respective localization cues. During the subsequent testing phase, participants in the boundary/landmark condition were tested with the original learning cue, without feedback; meanwhile, those in the compound-cue conditions were tested with one of the two cues removed. Localization performance was measured as the distance between the response locations (where participants placed the objects) and the corresponding correct locations.

The results revealed that participants in the compound-cue condition who were tested with the landmark alone (i.e., with the boundary removed) were less accurate in locating the objects during the testing phase compared to those in the landmark condition (in which the traffic cone was presented throughout learning and testing). Such inferior test performance was not observed in the compound-cue group who were tested with the boundary alone (i.e., with the landmark removed) in comparison to the boundary group (i.e., with the boundary presented throughout learning and testing). Hence learning locations relative to the boundary overshadowed learning locations relative to the single landmark when both cues were available in the environment. Participants, however, were able to use the landmark for localization when the landmark was the only cue available, as evident in the landmark condition. It is thus, proposed that boundary-related learning is incidental and is governed by the place learning mechanisms, whereas landmark-related learning obeys the rules of associative learning. Hence, according to the authors, the boundary advantage in encoding locations might be a result of the different learning mechanisms underlying localization relative to the two cues.

In addition to gaining accurate representations of individual locations, in order to successfully navigate in a large environment that is beyond one's vicinity, one has to integrate separate spatial memories (e.g., representations of individual locations) acquired at different points in time, and in different local spaces, into a unified representation of the environment, much like combining pieces of puzzles to make a whole picture. For example, knowing where one's office and the grocery store are spatially situated in relation to one's home will enable a successful trip between the office and the grocery store, even though one might never have travelled directly between the two locations before. Such integrated representations, which allow for inferring spatial relations among multiple locations (i.e., a vector between two locations that specifies direction and distance information), are called *cognitive maps* (Tolman, 1948; see also Nadel, 2013; Bennet, 1996). We refer to this integration process as *cognitive mapping*.

Although surface boundaries as a localization cue have been assigned a privileged role over object-based landmarks in encoding individual locations (e.g., overshadowing from a boundary over a landmark, but not vice versa, in goal localization), less is known regarding their roles in the cognitive mapping process. In one recent study, Zhou and Mou (2016) used both a novel-vector inference task (Experiment 1) and a configuration judgement task (Experiment 2) to assess the qualities of the cognitive maps derived from either a featureless circular boundary cue or a single landmark cue. Participants learned sequentially the locations of four objects in an immersive VR environment using either a circular wall (the boundary condition) or a traffic cone placed within the range of the boundary (the landmark condition). In addition to the localization cues, distal orientation cues were provided in both conditions. In the subsequent testing phase, the original localization cues were removed (the wall in the boundary condition and the traffic cone in the landmark condition, Experiment 1) or both the original localization and the distal cues were removed (Experiment 2). Instead, one of the four objects (Experiment 1) or two of the four objects (Experiment 2) was/were shown at its/their correct locations as the testing cues and participants were asked to place the remaining objects back while the distal orientation cues were kept. The tasks were thought to directly examine the relative quality of the cognitive maps derived from spatial learning based on the boundary/landmark.

The results revealed a less accurate cognitive map of the four locations, in terms of inferior inferences of novel spatial relations between two locations and inferior configuration judgment among three locations, derived from spatial learning relative to the boundary than to the landmark. Note that individual representations of the four locations acquired from the two cues were comparable, as revealed by equivalent accuracy in locating the four objects relative to either cue at the end of the learning phase. Thus, the inferior cognitive maps developed from the boundary-related spatial learning seem to be resulted from the differences in the cognitive mapping processes relative to the two cues.

To explain such single-landmark advantage in cognitive mapping (more accurate cognitive maps derived from the landmark cue), Zhou and Mou (2016, see also Zhou & Mou, 2017) proposed a vector addition model. The model posits that regardless of the underlying mechanisms, in order to successfully represent a location, a vector needs to be established between the location and a reference point chosen from the environment. When two locations are encoded relative to a common reference point (such as the single traffic cone), cognitive mapping is relatively simple, as one only needs to add the two individual vectors together (each vector encoding the spatial relation between the common reference point and one of the two locations) to infer the third vector between the two locations. However, when two locations are encoded relative to two distinctive reference points (one reference point per location), cognitive mapping is relatively more difficult, as one also needs to encode the spatial relation between the two chosen reference points and include this vector in the aforementioned addition process. The boundary cue (such as the circular wall) provides multiple reference points for encoding different locations within the enclosure (see also Mou & Zhou, 2013), leading to a more complex vector addition process during cognitive mapping.

The finding that a single landmark, rather than a boundary, was a more effective cue in cognitive mapping is surprising, given previous findings suggesting the superiority of the boundary over the single landmark (Doeller & Burgess, 2008; Mou & Zhou, 2013). Given the important role of the hippocampus rather than the striatal system in forming cognitive maps (O'Keefe & Nadel, 1978; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003; Ekstrom, et al., 2003; Hartley, Maguire, Spiers, & Burgess, 2003; Marchette, Bakker, & Shelton, 2011) and the control of boundaries over hippocampal activations, one would expect a more accurate cognitive map to be developed from the boundary cue.

The major goal of the current study is to reconcile the inconsistent findings regarding the differing advantages of a boundary cue and a landmark cue depending on the spatial tasks involved (Doeller & Burgess, 2008; Zhou & Mou, 2016). We hypothesize that *encoding individual locations* and *inferring spatial relations* among locations are two separate stages of cognitive-map formation. The advantage of a boundary cue occurs in the former stage, whereas the advantage of a single landmark occurs in the latter stage. Although Zhou and Mou provided the vector addition model to explain the better cognitive mapping relative to a single landmark than to a boundary, this model only works for inferring spatial relations.

The advantage of a boundary cue in encoding individual spatial locations might result from the perception that it provides "better" reference points to encode individual locations. Upon first encountering an environment, with a navigational goal in mind (e.g., to remember a certain location of interest), people evaluate the usefulness of different features provided in the environment in order to choose an appropriate cue to achieve their goal. Different weightings are then assigned to different environmental features depending on their evaluated usefulness, which determines the relative reliance upon a particular cue (Ratliff & Newcombe, 2008). In the case of encoding a particular location, it is likely that a distinctive and more peripheral feature of the environment will be favored as the reference point for the location. We refer to this process as reference-point selection. Spatial relations between the target and the selected reference point would then be established. We propose that two physical features of a boundary cue could potentially give rise to its advantage over a landmark cue in the selection of reference points.

First, a boundary cue, usually as a peripheral visual feature in the environment, might be preferred when adult participants are localizing in enclosed space. A bias towards more distal cues (e.g., the boundary of an environment) over proximal cues (e.g., intramaze landmarks) has been shown in several studies of reorientation behavior in humans (e.g., Redhead & Hamilton, 2007), as well as in some other animal species (e.g., Graham, Good, McGregor & Pearce, 2006; Kelly, Spetch & Heth, 1998). More relevant to the current project in which directional information was clearly provided by the distal orientation cues, placement of intramaze landmarks determines the preference for intramaze landmarks as reference points to encode a location. Specifically, more peripherally-placed intramaze landmarks, as compared to proximal ones, are more readily used to encode locations (O'Keefe & Nadel, 1978; Lew, 2011). Such shift in the status of intramaze landmarks as a result of their placement corresponds to the changes of underlying neuronal processes. Neurophysiological studies have shown that distal intramaze landmarks exert a stronger control over the hippocampal place cells (Cressant et al., 1997) as well as the head direction cells in the thalamus (Zugaro, Berthoz & Wiener, 2001), both of which support computation for spatial navigation (Jeffrey, 2010). More reliance on the peripheral intramaze landmarks might be due to that these landmarks are perceived as more stable or reliable because a) the peripheral landmarks are always visible when participants search for a goal, given their starting point and the correct starting direction based on distal orienting cues, and b) the sense relations (i.e. left or right) between different landmarks in different directions will not alter as participants move through the space (e.g. Lew, 2011; Save & Poucet, 2009).[1]

Second, a boundary cue based on a continuous surface could provide multiple distinctive reference points for encoding individual locations within the boundary. In our previous work, we proposed a probable localization process relative to a circular boundary together with distal orientation cues (Mou & Zhou, 2013; see also Zhou & Mou, 2016). For instance, when participants were localizing within the circular wall (Figure 1), the distal orientation cues allowed them to segment the continuous surface into differentiating parts (e.g., the segment closest to the north). Participants could then choose an appropriate wall segment (i.e., the segment closest to a target location compared to all the other segments) as the optimal reference point for a particular target location (e.g., the candle is five meters south of the North wall). Thus, each target location within the boundary could be associated with a unique reference point (a wall segment distinguished by an aligning distal orientation cue). By contrast, a single landmark could only serve as a common

[1] We are grateful to an anonymous reviewer for the suggestions of these two reasons.

reference point for encoding a set of locations, which would cause potential interference in location representation and retrieval. This postulate is inspired by the interference theory in associative learning and memory literature (for a brief review see Anderson, 2003), which proposed that forgetting can be induced by adding a new memory trace to an old retrieval cue. Hence a single landmark would be evaluated as a less useful cue for encoding multiple locations than a boundary that provided distinctive reference points. Consequently, in order to ensure that representations of individual locations would be unique from each other (thus less interference), distinctive environmental cues would be favored.

[Figure 1 here]

The first purpose of the current study was to test the two-stage model in a single study. While both the superiority of boundaries over landmarks in goal localization and the superiority of landmarks over boundaries in cognitive mapping were reported in the previous studies, there is no study that demonstrates both effects in a single study to directly contrast these two effects, by strictly minimizing any possible differences other than the key manipulations that lead to the two effects. The second purpose was to test the potential contributions of the aforementioned factors in modulating the relative degree of reliance upon a boundary and a landmark in encoding individual locations.

Experiment 1 is divided into two separate studies to further test the two-stage model of localization within a single study. In Experiments 2-4, using the same cue-competition paradigm, we manipulated the cue placement and the distinctiveness of the landmark array to examine whether and how the two factors modulate the degree of reliance upon the two cues during the cue-selection process.

Experiment 1

Experiment 1A

A localization task was employed to assess the relative advantages of a boundary cue and a landmark cue in encoding individual locations. Specifically, a circular wall as the boundary and a landmark array comprising four traffic cones of identical appearance were presented as the localization cues. Each landmark in the array was intentionally paired with one of the four target locations so that the distance between one landmark and its corresponding target location was the same as the shortest distance between that particular location and the boundary (for detailed illustrations see Figure 2). In this way, we eliminated the differences between the circular wall and the four-landmark array in terms of their distance to the four targets and the number of reference points. Our previous work (Zhou & Mou, 2017) suggests that participants likely choose four optimal reference points (segments of the boundary closest to target locations) for encoding four target locations, respectively, within a circular boundary. By matching the number of landmarks in the array as well as the distance between targets and references (the landmark array/the boundary), we aimed to set the two cues comparably informative of the target locations. However because the wall is placed more peripheral than the intra-maze cone array in the environment, we hypothesize that a superiority of the boundary over the landmark array will still be observed when two cues are presented simultaneously.

Participants learned the locations of four objects sequentially, in the presence of both a circular wall (the boundary) and a cone array consisting of four identical traffic cones (the landmark). In the subsequent testing phase, one of the two cues (the circular wall or the cone array) was removed and participants were asked to replace the four objects based on the remaining cue.

Relative accuracy of the localization performance during testing compared to that during learning was thought to reflect the degree of reliance upon the remaining cues.

Method

Participants. 48 students (24 females) from the University of Alberta participated to fulfill a course requirement. When only the landmark was available as the localization cue in the environment (e.g., during the testing phase when the boundary was removed), participants could freely move beyond the range of the circular wall which is no longer present. Due to the lack of this constraint, a criterion was set before carrying out the study that participants with mean response errors larger than 100 virtual meters (vm) would be excluded (the boundary was 50 vm in radius). No participants were excluded in this experiment.

Materials and Design. An immersive virtual environment was displayed using an nVisor SX60 head-mounted display (HMD) (NVIS Inc., Virginia). Graphics were rendered using Vizard software (WorldViz, Santa Barbara, California). Head orientation was tracked with an InterSense IS-900 motion tracking system (InterSense Inc., Massachusetts). Thus, through head rotation, participants could change their viewpoints. Participants used a joystick to translate, to pick up and to replace objects in the virtual environment.

In the virtual environment (Figure 2A), participants learned four locations on infinite grassland by picking up four sequentially presented objects (a candle, a lock, a bottle and a wood block) and then placing them in the correct locations. A fixed set of locations was used for all of the participants; however, the object-location pair was randomized across participants. During the learning phase, both a visually homogeneous, circular wall (the boundary cue) and a cone array consisting of four identical traffic cones (the landmark cue; each traffic cone was visually homogeneous as well, illustrated as the triangles in Figure 2A) were presented as the localization cues. Four different scenes (ocean, forest, mountain and city) were set at an infinite distance from participants as distal orientation cues (indicated by the surrounding labels in Figure 2). In the testing phase (Figure 2B), for half of the participants, the circular boundary was removed and the participants were asked to place the objects to their correct locations based on the remaining cone array and the distal orientation cues (this condition is referred to as LB-L). For the remaining half of participants (Figure 2C), the cone array was removed during testing, and the participants were asked to replace objects based on the remaining circular wall and the distal orientation cues (this condition is referred to as LB-B).

Each traffic cone in the cone array was (unknown to the participants) intentionally paired with one of the four locations so that the distance between one cone and its corresponding target location was the same as the shortest distance between this particular location and the circular wall (for detailed illustrations see Figure 2). In addition, each traffic cone was also intentionally placed as far inwards from the circular wall as possible while still maintaining a distance from the other three unpaired locations. Hence the overall distance between the landmark array and the four locations was smaller (averaged across the four locations) than the overall shortest distance between the wall and the four locations. Previous research has demonstrated that a landmark closer to a target location has more control as a reference point than a further-away landmark for encoding the particular location (Cheng, 1989; Spetch, 1995). One question we were also interested in was whether this increased proximity of the landmark cue to the target locations could modulate the relative weightings assigned to the two cues, leading to an increased reliance upon the landmark cue. In this case, the landmark cue would be superior over the boundary cue as a result of proximity of the landmark array to the target locations.

[Figure 2 here]

Procedure. Participants donned the HMD and sat on a swivel chair at the center of the experiment room. Each participant went through three phases: the pick-up phase, the learning phase and the testing phase. During the pick-up phase, participants collected the four objects one by one from the objects' original locations. The learning phase comprised four blocks of four learning trials (one trial per object in each block). During each learning trial, one of the four objects was probed, and participants replaced the probed object using their memory of its original location. After the response, the probed object appeared at its correct location. Participants were asked to collect it (this served as feedback, allowing participants to learn the locations in a trial-and-error fashion). Participants' starting locations (could be anywhere within a range of 40 virtual meters from the center of the wall) and facing directions at the beginning of each trial were randomized. During the testing phase, the circular wall in LB-L and the cone array in LB-B were removed; the orientation cues, however, remained. With the exception of the removal of cues according to the conditions, the testing phase was conducted in exactly the same way as the learning phase. Participants replaced each of the four objects once in each block (thus four trials per block), over a total of four blocks. No feedback was given in the testing phase.

Results

Response errors, measured as the distances between participants' response locations and the corresponding correct locations, were recorded as the dependent variable for all of the experiments in the study.

We analyzed the impairment effect by comparing the response errors of each participant in the testing phase with the response error of the same participant in the learning phase. Increased response errors in the testing phase compared to those in the learning phase would indicate an impairment effect resulting from the removal of one of the two cues, which would be equivalent to a typical overshadowing effect. We were also interested in the relative degree to which such an effect would result from the removal of either of the two cues, if we did observe increased response errors during testing in both LB-B and LB-L. As noted above, the particular arrangement of the cone array in the current experiment might increase the relative weight on the landmark array compared to that of the landmarks used in the previous experiment (e.g., Doeller & Burgess, 2008; Mou & Zhou, 2013), which might lead to an impairment effect resulting from the removal of the cone array in LB-B. If a bi-directional overshadowing effect was observed, the relative degree of the two impairment effects (i.e., whether the increase in response errors in LB-L was larger than that in LB-B) might indicate the relative weightings assigned to the two cues.

Across the four learning blocks, there was a significant learning effect through feedback (Figure 3A), $F(3, 138) = 12.65$, $MSE = 44.78$, $p < .001$, $\eta_p^2 = .22$. Across the four testing blocks, however, there was no learning effect (Figure 3B), $F(3, 138) = .27$, $MSE = 55.70$, $p = .85$, $\eta_p^2 = .006$. This was expected, as no feedback was provided in the testing blocks. Similar results were observed in the subsequent experiments. Hence, only the response error in the last learning block was compared to the response error in the four testing blocks in this experiment and in Experiments 2 and 3. The mean response errors were averaged in the last learning block and in the four testing blocks for each participant.

[Figure 3 here]

The mean response errors are plotted as a function of condition (LB-L vs. LB-B) and experimental phase (last learning block vs. all testing blocks) in Figure 4. The mixed-model

ANOVAs were conducted to analyze the impairment effect from removing different cues, with condition (LB-L vs. LB-B) as a between-subject variable and experimental phase (the 4th learning block vs all testing blocks) as a within-subject variable. An interaction between condition and experimental phase was revealed, $F(1, 46) = 6.52$, $MSE = 67.00$, $p = .014$, $\eta_p^2 = .12$, as well as a main effect of experimental phase, $F(1, 46) = 19.54$, $MSE = 66.70$, $p < .001$, $\eta_p^2 = .30$. The main effect of condition was not significant, $F(1, 46) = 1.33$, $MSE = 123.12$, $p = .26$, $\eta_p^2 = .03$. Planned comparisons indicated that response errors increased significantly during the testing phase in LB-L, $t(23) = 4.93$, $p < .001$, Cohen's $d = 1.42$ ($M_{4th\_learning\ block}$ = 16.44 vm, $SD_{4th\_learning\ block}$ = 6.84; $M_{testing\_average}$ = 28.10 vm, $SD_{testing\_average}$ = 14.86), whereas the response errors during the testing phase in LB-B did not differ significantly from those during the last learning block, $t(23) = 1.32$, $p = .2$, Cohen's $d = 0.38$ ($M_{4th\_learning\ block}$ = 18.10 vm, $SD_{4th\_learning\ block}$ = 8.76; $M_{testing\_average}$ = 21.22 vm, $SD_{testing\_average}$ = 6.00)

These results indicated that the superiority of the boundary cue over the landmark array in encoding individual locations. Even though in the current setup, four optimal landmarks were used, a boundary advantage in encoding individual locations was still observed.

[Figure 4 here]

Experiment 1B

A cognitive mapping task was employed to assess the relative accuracy of the cognitive maps derived from a boundary cue and from a landmark array. Instead of probing participants' memory of target locations based on the learned localization cue (the boundary or the landmark), the task request participants to extrapolating new spatial relations based on established cognitive maps. The superiority of a landmark in cognitive mapping and the superiority of a boundary in reference point selection for encoding individual locations had previously been reported in separate studies (Mou & Zhou, 2013; Zhou & Mou, 2016) varying in many uncontrolled variables (such as potential differences in the recruited samples of the two separate experiments with significant time span in between). By demonstrating the two effects in the same study, we assured that the relative advantages of a boundary cue and a landmark cue in encoding individual locations and in cognitive mapping were caused specifically by the different tasks. Furthermore, we used four landmarks instead of one landmark in the current experiment.

Participants learned the locations of four objects sequentially, using as a localization cue either the circular wall (the boundary condition) or the cone array (the landmark condition). During the subsequent testing phase, they were asked to infer the spatial relations between two of the four locations based on their representation of the individual locations. Localization performance during testing was thought to reflect the quality of cognitive maps derived from the respective learning cues.

Method

Participants. 48 students (24 females) from the University of Alberta participated to fulfill a course requirement. A criterion was set before the study that participants with mean response errors larger than 100 virtual meters (vm) would be excluded (the boundary was 50 vm in radius). No participant was removed from data analysis.

Materials and Design. The experimental setup was mostly similar to that in Experiment 1B, with the following exception. Participants were randomly assigned to two conditions which differed in terms of the localization cue presented during the learning phase. One group of participants (Figure 2C) learned the four locations relative to the circular wall (the same wall used in Experiment 1A), together with the distal orientation cues. We referred to this condition as B. The other group (Figure 2B) learned the four locations relative to the four-cone array (the same traffic-cone array used in Experiment 1A), together with the distal orientation cues. We referred to this condition as L.

During the testing phase (Figure 2D), the wall in B and the cone array in L were removed. However, one of the four objects was presented in each trial as the localization cue, together with the distal cues. Participants needed to replace the other three objects. Because participants never saw the four objects simultaneously, the vectors between the cue objects and the probed objects had to be a product of cognitive mapping. Therefore, participants' testing performances in L or B reflected the relative accuracy of cognitive mapping in each condition.

Procedure. The procedure was most similar to that in Experiment 1A, with the following exception. During the pickup and the learning phase, depending on the assigned conditions, participants were presented with either the circular wall (B) or the cone array (L) as the localization cue whereas the distal cues provided orientation information. During testing, the wall in B and the cone array in L were removed. At each testing trial, one of the four objects was shown at its correct location as a localization cue together with the distal orientation cues; participants replaced one of the other three objects. The testing phase comprised four blocks of three testing trials. In each block, one of the four objects served as the testing cue in all three trials, and each of the other three objects was probed once.

Results

The mean response error during the last learning block and the mean response error during the testing phase were examined separately, as we were interested in the relative quality of the cognitive maps derived from the respective learning cues between the two conditions.

The mean response errors of the last learning block were plotted as a function of learning-cue condition (L vs. B) in Figure 5. To ensure that participants in the two conditions acquired comparable representations of individual locations from respective localization cues after the learning phase, a one-way ANOVA was conducted on the mean response errors of the last learning block, with learning-cue condition as the between-subject variable. Participants in the two groups did not differ in terms of their localization accuracy at the end of the learning phase, $F(1, 46) = .0002$, $MSE = 97.68$, $p = .99$, $\eta_p^2 < .001$ ($M_{L\text{-learning}} = 20.17$ vm, $SD_{L\text{-learning}} = 11.20$; $M_{B\text{-learning}} = 20.21$ vm, $SD_{B\text{-learning}} = 8.36$, units in virtual meters [vm]). Thus representations of individual locations in the two conditions were comparable.

The mean response errors across four testing blocks were plotted as a function of learning-cue condition (L vs. B) in Figure 5. A one-way ANOVA was conducted to examine the relative quality of cognitive maps derived from the two conditions. A main effect of learning-cue condition was revealed, $F(1, 46) = 6.59$, $MSE = 368.57$, $p = .01$, $\eta_p^2 = .13$ ($M_{L\text{-testing}} = 33.40$ vm, $SD_{L\text{-testing}} = 11.14$; $M_{B\text{-testing}} = 47.63$ vm, $SD_{B\text{-testing}} = 24.76$). Thus participants who learned the locations relative to the landmark array developed a more accurate cognitive map, in terms of inferring spatial relations between two locations, than those who learned relative to the boundary.

[Figure 5 here]

Discussion

Experiments 1A and 1B confirmed the two-stage model of encoding objects' locations, demonstrating a boundary advantage over the four-landmark array in encoding and representing individual locations, as well as an advantage in using the landmark cue for the cognitive mapping of novel spatial relations.

Note that the boundary advantage does not correspond to a higher accuracy in localization relative to the boundary cue if only one cue is presented, as the results of Experiment 1B (i.e. the 4th learning block in Figure 5) clearly indicated that the representations of individual locations acquired from either of the two cues were equally accurate. We hypothesize that the boundary advantage (see Figure 4) might have been prominent during the reference-point selection process at the initial stage of goal localization when both cues were presented in Experiment 1A. By contrast, participants in Experiment 1B only saw one type of cue, so they did not engage in the reference-point selection process (selecting boundaries or landmarks). Therefore, the representations of individual locations acquired from the landmark array were as accurate as those acquired from the boundary (see Figure 4A). The advantage of the landmark cue over the boundary cue in cognitive mapping was still prominent (see Figure 4B) even though the cone array also provided multiple reference points (one for each target location) for encoding individual locations, which might be because encoding straight-line spatial relations among the four reference points was easier when the reference points were four discrete cones than when the reference points were four boundaries pieces (Zhou & Mou, 2017).

The preference for the boundary cue during the reference-point selection process at the initial stage of goal localization might be due to the perceived physical characteristics of the boundary, such as the boundary being more peripheral in the environment. In the following three experiments, we examined how cue placement could influence cue preference in goal localization.

Experiment 2

As we proposed in the Introduction, the spatial placement of a boundary cue (i.e., usually more peripheral in a given environment) and the distinctiveness of the multiple reference points provided by the boundary could be key factors modulating the preference for the boundary cue over a landmark cue (i.e., more weightings/reliance are assigned to the boundary when participants are selecting reference points for encoding locations). In Experiment 2, we arranged the intra-maze landmark array in a way that each cone in the array was moved outwards and closer to the circular wall). We did so in an effort to render the landmark array more peripheral, as well as make each cone more distinguishable from one another as a result of being further apart from each other.

Participants learned the locations of four objects with the presence of both a circular wall (as that in Experiment 1A) and a landmark array consisting of four identical traffic cones placed outwards (Figure 6A). During the testing phase, one of the two cues was removed. Representations of individual locations were tested with the remaining cue depending on the conditions.

Method

Participants. 48 (24 males and 24 females) students from the University of Alberta participated to fulfill a course requirement. No participant was removed from data analysis.

Materials, Design, and Procedure

The materials, design, and procedure were similar to those employed in Experiment 1A, except that each of the four traffic cones was moved towards the circular wall while the distance between each cone and its corresponding target location was maintained (see triangles in Figure 6A). Thus, for each target location, there was one optimal reference point available from the circular wall (the point closest to a particular target location from all the points on the wall) as well as from one of the four traffic cones at an equal distance. The group that was tested with the boundary alone was referred to as 4PLB-B (PL standing for *Peripheral Landmark*) and the group tested with the landmark array alone was referred to as 4PLB-4PL (Figure 6B).

[Figure 6 here]

Results and Discussion

The mean response errors are plotted as a function of condition (4PLB-B vs. 4PLB-4PL) and experimental phase (last learning block vs. all testing blocks) in Figure 7. Mixed-model ANOVAs were conducted to analyze the impairment effect resulted from the removal of different cues, with condition as a between-subject variable and experimental phase as a within-subject variable. The analysis revealed a main effect of experimental phase, $F(1, 46) = 24.01$, $MSE = 18.37$, $p < .001$, $\eta_p^2 = .34$, but the interaction was not significant, $F(1, 46) = .0001$, $MSE = 18.37$, $p = .99$, $\eta_p^2 < .001$, nor was the main effect of condition, $F(1, 46) = .92$, $MSE = 70.01$, $p = .34$, $\eta_p^2 = .02$. Hence removing either of the two cues, the boundary or the outward landmark array, impaired localization during testing; and more importantly, the degree of impairment resulting from the removal of either cue was not significantly different, as indicated by a lack of interaction. It is likely that both the boundary and the landmark array were relied upon equally as the reference points for encoding the four locations.

[Figure 7 here]

Experiment 3

Moving landmarks to more peripheral locations in Experiment 2 not only changed cue placement but also could increase distinctiveness of a landmark cue. When landmarks were moved to peripheral locations, they were further away from each other (see Figure 2A and Figure 6A) and therefore more distinctive from each other. Hence, it is not clear whether distinctiveness alone or cue placement alone could modulate the relative preference for a landmark as a reference point for encoding locations. In Experiment 3, we increased the distinctiveness of each traffic cone in the cone array compared to those in Experiment 1A. If the distinctiveness alone could explain the increased reliance upon the landmark cue in Experiment 2, we would expect a similar pattern of bi-directional impairment effects to result from removing either cue in the current experiment. Alternatively, if cue placement (peripheral or not) is essential in modulating reference-point selection, we would expect a pattern similar to the boundary advantage found in Experiment 1A.

Participants learned the locations of four objects with the presence of both a circular wall (the one presented in Experiment 1A) and a landmark array consisting of four identical traffic cones (at the same locations as those used in Experiment 1A). However, the four cones were not presented simultaneously during each learning trial (Figure 6C). Instead, depending on the target location to be learned in a particular learning trial, one corresponding traffic cone (always the one that was closest to the target location among the four cones) would be presented together with a unique visual feature added on top of the cone. Therefore, the association between one landmark and one target location would not interfere with the association between another landmark and another target location. During the testing phase, one group was tested with the boundary alone; this condition was referred to as 1DLB-B (DL standing for *Distinctive Landmarks*). The other group was tested with the four cones presented simultaneously (each traffic cone still had the unique visual feature on top to maintain its distinctiveness); this condition was referred to as 1DLB-4DL.

Method

Participants. 25 students (12 males and 13 females) from the University of Alberta participated to fulfill a course requirement. One female participant was excluded, as her mean response error during testing was greater than 100 vm.

Materials, Design, and Procedure. The setup of Experiment 3 was identical to that of Experiment 1A, with the following exceptions.

During the pick-up phase, the four cones were presented simultaneously, and each traffic cone had a small model of one of the four objects on top, which was used to make each cone identifiable from the others. The identity of the small objects on top of each cone depended on the identity of the target object (the candle, the wood, the bottle or the lock) whose location was paired with the particular traffic cone. During the learning phase, at each trial, depending on the target location to be learned at the trial, only the corresponding traffic cone (the closest one among the four to this particular target location) would be presented together with the corresponding small object model on top of the cone. The circular wall as the boundary cue was also presented throughout the pick-up and the learning phase for each participant.

During the testing phase, one group of participants was tested with the boundary cue alone (the cone array removed). For the other group, the boundary cue was removed but the four cones with their respective object models on top were presented throughout the testing phase.

Results and Discussion

The mean response errors are plotted as a function of experimental phase (the 4th learning block vs. all the testing blocks) and condition (1DLB-4DL vs. 1DLB-B) in Figure 8. Mixed-model ANOVAs were carried out to examine the impairment effect resulted from removing either cue during testing, with experimental phase as a within-subject variable and condition as a between-subject variable. An interaction between the variables was revealed, $F(1, 22) = 5.21$, $MSE = 52.51$, $p = .03$, $\eta_p^2 = .19$, as well as a main effect of experimental phase, $F(1, 22) = 13.65$, $MSE = 52.51$, $p = .001$, $\eta_p^2 = .38$. The main effect of condition was not significant, $F(1, 22) = .7$, $MSE = 80.47$, $p = .41$, $\eta_p^2 = .03$. Planned comparisons indicated a significant increase in response errors during the testing phase of 1DLB-4DL compared to the last learning block, $t(11) = 4.23$, $p = .001$, Cohen's $d = 1.73$ ($M_{4th\ learning\ block} = 16.08$ vm, $SD_{4th\ learning\ block} = 8.54$; $M_{testing\ average} = 28.59$ vm, $SD_{testing\ average} = 11.19$), whereas the response errors during testing were not significantly different from those during the last learning block in 1DLB-B, $t(11) = 1.00$, $p = .34$, Cohen's $d = .41$ ($M_{4th\ learning\ block} = 18.69$ vm, $SD_{4th\ learning\ block} = 6.72$; $M_{testing\ average} = 21.65$ vm, $SD_{testing\ average} = 4.76$).

Hence removing the boundary cue during testing impaired localization; however, removing the landmark array did not have such an impairment effect on localization. This replicated the findings of Experiment 1A, suggesting that participants seemed to assign their encoding resources to more peripheral environmental feature rather than more distinctive landmarks.

[Figure 8 here]

Experiment 4

We demonstrated in Experiment 3 that participants still preferred to use a boundary rather than an intra-maze landmark array as a reference for encoding locations, even though the landmark array could provide highly distinctive reference points for discerning multiple location memories.

However, our manipulation of the cone array (specifically, making only one cone available at each learning trial) in Experiment 3 might potentially diminish the perceived stability of the landmark cue, and participants might consequently consider it as less reliable for encoding other locations (Knierim, Kudrimoti & McNaughton, 1995). We designed Experiment 4 to exclude this confounding possibility in an attempt to provide a more direct comparison between the relative influence of cue placement vs. cue distinctiveness on the weighting process involved in reference-point selection. The setup was mostly identical to that in Experiment 3 however the cone array was presented throughout the learning phase.

Method

Participants. Twenty-four students (12 females) from the University of Alberta participated to fulfill a course requirement. No participant was removed from data analysis.

Materials, Design, and Procedure. The setup of was identical to that of Experiment 3, with one exception. The four-cone array, together with the distinctive object labels on top of each cone, was presented throughout the learning phase. Participants were randomly assigned to one of the two conditions where one of the two learning cues (the wall or the 4-cone array) was removed during testing: 4DLB-4DL (tested with the 4-cone array alone) and 4DLB-B (tested with the wall alone).

Results and Discussion

As Experiment 3, the mean response errors are plotted as a function of experimental phase (the 4th learning block vs. all the testing blocks) and condition (4DLB-4DL vs. 4DLB-B) in Figure 9. Mixed-model ANOVAs were carried out to examine the impairment effect resulted from removing either cue during testing, with experimental phase as a within-subject variable and condition as a between-subject variable. An interaction between the variables was revealed, $F(1, 22) = 7.119$, $MSE = 35.37$, $p = .014$, $\eta_p^2 = .17$, as well as a main effect of experimental phase, $F(1, 22) = 13.015$, $MSE = 35.37$, $p = .002$, $\eta_p^2 = .31$. The main effect of condition was not significant, $F(1, 22) = .001$, $MSE = 187.15$, $p = .98$, $\eta_p^2 < .001$. Planned comparisons indicated a significant increase in response errors during the testing phase of 4DLB-4DL compared to the last learning block, $t(11) = 4.44$, $p < .001$, Cohen's $d = 1.81$ ($M_{4th\ learning\ block} = 14.37$ vm, $SD_{4th\ learning\ block} = 8.63$; $M_{testing\ average} = 25.14$ vm, $SD_{testing\ average} = 14.63$), whereas the response errors during testing were not significantly different from those during the last learning block in 4DLB-B, $t(11) = 0.66$, $p = .51$, Cohen's $d = .27$ ($M_{4th\ learning\ block} = 18.82$ vm, $SD_{4th\ learning\ block} = 9.71$; $M_{testing\ average} = 20.43$ vm, $SD_{testing\ average} = 7.89$).

Again, we observed a uni-directional impairment effect in location memories when the boundary, rather than the intra-maze landmark array, was removed during testing, even though we increased the stability of the landmark cue as compared to that in Experiment 3. The results of Experiment 3 and 4 combined suggested the distinctiveness of potential reference points from an environmental feature alone was not sufficient to modulate the relative preference assigned to a landmark cue and a boundary in encoding individual locations; the spatial placement of a feature (peripheral vs more centrally placed within a given environment) was critical in the evaluation of its usefulness as a potential reference point for encoding locations.

[Figure 9 here]

General Discussion

Four experiments were conducted to examine the potential factors contributing to the boundary advantage in encoding/representing individual locations, and in particular the spatial placement of an environmental feature and the distinctiveness of the potential reference points provided by the environmental feature for encoding a set of locations. Experiment 1A and 1B replicate both the boundary privilege in encoding individual locations (the boundary cue overshadowed the four-cone array but not vice-versa) and the landmark-array advantage in cognitive mapping. Experiment 2 demonstrate that moving the landmark-array to more peripheral locations could increase the relative reliance upon the landmark cue when both the boundary and the landmark were available as potential reference points for encoding locations. However, when the four cones are made further away from each other (as a result of expanding the array towards the periphery), each individual reference point within the landmark array are likely to be more discernible from each other. Experiment 3 and 4 thus further examined whether the distinctiveness among multiple reference points is sufficient to explain the increased bias towards the landmark array observed in Experiment 2. The results suggest that increasing distinctiveness alone was insufficient to modulate the reference-point selection process as indicated by the impairment effect from removing the circular boundary but the lack of impairment effect from removing the 'distinct' cone-array. Combining the last three experiments, we conclude that cue placement (peripheral vs. proximal), rather than cue distinctness, is more critical in modulating the selection bias towards certain environmental features in a localization task.

Why are environmental features placed at the periphery more readily used for computing locations? Peripheral features tend to remain visually invariant from different vantage points when one navigates through local space. As a result, they provide more reliable directional information (O'Keefe & Nadel, 1978). However, in the current study, directional information was clearly indicated by the distal orientation cues (e.g. the city). Then, why are peripheral features still preferred for encoding locations? One possible reason is that peripheral features could provide stable reference points for encoding locations (Lew, 2011; Save & Poucet, 2009). For example, the leftmost landmark in Figure 6A could be visible at most viewpoints as long as participants face left based on the distal orientation cues (e.g. the direction between the forest and the city in Figure 6A). In contrast, proximal landmarks could be invisible from many viewpoints given a viewing direction based on the distal orientation cues. For example, the leftmost landmark in Figure 2A could be invisible at nearly half of the viewpoints when participants face left.

Experiment 1 demonstrates that flexible location coding could be derived from an intramaze landmark array as probed in a spatial task where novel spatial relations had to be inferred. The finding that discrete landmarks can facilitate cognitive mapping is consistent with the position that navigational function of discrete landmarks varies depending on the environmental context (e.g., cue placement) and navigational goals (Chan, Baumann, Bellgrove & Mattingley, 2012). Because the cognitive mapping task employed in Experiment 1B required flexible location coding relative to the landmark array and given that it was the only available local feature in the landmark condition, participants had to derive spatial vectors (direction and distance) from the landmark cue to encode the target locations. There is evidence showing that such spatial learning relative to discrete objects is supported by the hippocampal systems (Wegman, Tyborowska, & Janzen, 2014). Hence, we speculate that there could be multiple neural systems underlying landmark-related processing, depending on the strategy involved in solving a particular spatial task. In particular, landmark-related learning might elicit stronger striatal activations when the landmark serves as an associative cue in cue-response learning (e.g., Doeller, King & Burgess, 2008; Chan, Baumann, Bellgrove & Mattingley, 2012) whereas flexible location coding relative to landmarks might be computed in the hippocampal systems.

One alternative explanation for the one-directional impairment effect observed in the current experiments (except Experiment 2) could be that participants' movement was no longer restricted once the boundary was removed. We acknowledge that our current design (compound-cue during learning and single-cue during testing) is not sufficient to address this confounding effect of generalization decrement. However, in our previous study (Mou & Zhou, 2013), we replicated the classical overshadowing effect of a boundary cue over a landmark cue. In one of the experiments, we trained participants to localize four target objects with respect to a boundary alone, a landmark alone (the two single-cue conditions) or to both cues (compound-cue conditions; Exp. 1). In the subsequent testing phase, participants in the two single-cue conditions recalled location memories with the same learning cue whereas in the two compound-cue conditions, either the boundary or the landmark was removed and participants had to localize with the remaining cue. Localization performance decreased in the testing phase of the compound-cue condition when participants was tested with the landmark alone whereas there was no decrease of performance in the single-cue condition when participants learned and tested with the landmark throughout. In addition, when we increased the number of landmarks in the intra-maze landmark array with the same overshadowing paradigm, there was no overshadowing effect from removing either cue (Exp. 2 of Mou & Zhou, 2013). Note that in this condition, participants could freely move outside of the landmark array during testing. Taking these results together as a partial support, we reasoned that movement constraint alone would not be sufficient to explain the presence/absence of the impairment effect. But rather, the characteristics of the landmark/boundary might modulate the effect.

Strikingly, the results of Experiment 2 showed that learning locations relative to a landmark array, which was placed close to the boundary, could impair the simultaneous learning of the same locations relative to a boundary cue. This finding challenges the proposal that boundary-related learning is incidental. Our result suggests that boundary-related learning might also be subject to the reference-point selection process, during which participants evaluate different environmental features to choose adequate reference points for encoding a particular location. Moreover, the relative reliance upon a certain environmental feature (or the relative weighting assigned to a certain environmental feature during reference-point selection) seems to be modulated by the physical characteristics of the feature, such as its spatial placement in the environment. In the current study, when the four-cone array was moved towards the periphery, participants might have been more likely to evaluate the cones as adequate candidate reference points for encoding locations. As a result, bi-directional cue competition between the cone array and the circular boundary was observed.

Furthermore, the total computational resources devoted to learning locations relative to different environmental cues seems to be limited, as suggested by the reduced reliance upon the boundary cue when the landmark cue was placed more peripheral in the environment in the current study. This is in line with the associative model of geometry learning in reorientation (Buckley et al., 2014; Miller & Shettleworth, 2007). Abundant findings in reorientation literature have suggested that the geometric information provided by a surface boundary plays a privileged role in helping animals keep their bearings (for review of findings across different species, see Cheng & Newbombe, 2005). Thus the learning of surface geometry provided by a boundary was thought to be exclusive of learning related to other environmental features. However, later evidence challenged the impenetrable characteristics of learning surface geometry, in that such learning was shown to be hindered or facilitated by learning of other environmental features (Buckley et al., 2014; Pearce, Graham, Good, Jones & McGregor, 2006; Wilson & Alexandar, 2008, 2010). Miller and Shettleworth adapted the Rescorla-Wagner model in associative learning to account for the inconsistent findings regarding cue competition between a boundary cue and other environmental features. According to their model, associative strength is assigned to enclosure geometry in terms of the probability that the cue can predict a reward location, and the strength is subject to competition from other environmental features.

Although the current task is a localization task, we propose that a similar weighting process also happens at the initial stage of navigation process in general when people evaluate different environmental features according to the physical characteristics of the features and the navigational goal they have in mind. The idea of the cue evaluation process is in line with the adaptive combination model proposed by Newcombe and colleagues (Ratliff & Newcombe, 2008; see also Cheng, Huttenlocher, & Newcombe, 2013). For instance, a peripheral environmental feature will be evaluated as a better reference point for encoding a target location. Once the environmental cues are selected as reference points for encoding locations, computational resources are devoted to spatial learning relative to the chosen reference point. Such an evaluation and reference-selection process is also involved in boundary learning. In the present study, therefore, when the landmark array was evaluated as a competitive cue for localization, less weighting might have been assigned to encoding relative to the boundary, which led to an overshadowing effect from the landmark array over the boundary. The current study only used a circular boundary and manipulated the spatial placement and the distinctiveness of the two cues. Future studies are needed to look into other factors that could modulate the reference-point selection process, such as the shape of the boundary or the configuration of the landmark array.

In conclusion, the current study demonstrated a boundary advantage in encoding individual locations as well as a landmark advantage in cognitive mapping (Experiment 1). Moreover, we found that cue placement can modulate the boundary advantage in encoding individual locations (Experiment 2-4)—that is, spatial learning relative to an intra-maze landmark placed more peripherally in an environment can impair spatial learning relative to a continuous boundary, and the magnitude of such an effect is equivalent to that from the boundary, demonstrating that the two cues compete equally for the computational resources assigned to learning them.

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Figure Captions

Figure 1. Schematic illustration of the process of encoding a single location relative to a circular homogeneous boundary. The target location is illustrated as the dot within the circle. The four shapes represent distal orientation cues. The two dashed lines illustrate segmentation based on the distal orientation cues, and the red wall segment represents the optimal reference point for encoding the target location. The dotted arrow illustrates the vector established between the location and the chosen wall segment.

Figure 2. Top-view illustrations of the virtual environments used in Experiment 1. A, The learning phase of Experiment 1A. The circle illustrates the wall, 50 virtual meters (vms) in radius, which is also illustrated as the dashed line in the circle. The two dotted lines with arrows illustrate the coordinate axes where (0, 0) is the origin of the coordinate system (and the center of the wall) used in the virtual-reality environment. The axes and the center are marked only for readers. The four dots illustrate the target locations. The coordinates of the four locations are (35.86, 19.88), (-7.74, -31.05), (-5.14, 6.13), and (-18.02, -12.62) (units in vms). The four labels (Ocean, Mountain, City, and Forest) illustrate the background scenes set at an infinite distance from the center of the environment. The four-cone array is illustrated as the four red triangles. The dotted lines reveal that the shortest distance from each of the four locations to the circular wall is equivalent to one of the traffic cones paired with the particular location (these dotted lines were not marked in the experiment and participants were not aware of the pairings). The coordinates of the four traffic cones are (25.96, 13.08), (7.69, -21.78), (34.32, -8.24), and (-3.04, -8.29,); B, The testing phase of LB-L (the circular wall removed) in Experiment A1 as well as the learning phase of L in Experiment 1B; C, The testing phase of LB-B in Experiment 1A as well as the learning phase of B in Experiment 1B; D, The testing phase of both conditions (B and L) in

Experiment 1B. The dot illustrates one of the four objects at its original location used as the testing cue for one particular trial. The original localization cue (the landmark or the boundary) was removed.

Figure 3. Response errors as a function of condition (LB-L or LB-B) and progress of blocks (1-4) in Experiment 1A. A, throughout the learning phase; B, throughout the testing phase. Error bars are ± 1 standard error.

Figure 4. Response errors as a function of condition (LB-L or LB-B) and experimental phase (the fourth learning block or the average of all the testing blocks in the testing phase) in Experiment 1A. Error bars are ± 1 standard error.

Figure 5. Response errors during the fourth learning blocks, and response errors during the testing phase, as a function of learning-cue condition (L or B) in Experiment 1B. Error bars are ± 1 standard error.

Figure 6. Top-view illustrations of the virtual environments used in Experiment 2 and 3. A, The learning phase of Experiment 2. The four traffic cones (the same as those used in Experiment 1) were placed further outwards and closer to the wall than those in Experiment 1. Each traffic cone was kept at the same distance from its paired target location, which was the shortest distance from the particular target location to the wall. The coordinates of the four traffic cones were (37.27, 10.99), (9.72, -35.40), (27.03, 33.13), and (-45.60, -7.76), respectively; B, The testing phase of 4PLB-4PL (with the circular wall removed) in Experiment 2; C, The learning phase in Experiment 3. The circular wall as well as one of the four traffic cones was presented at a particular learning trial. The identity of the presented traffic cone varied across trials, depending on the target location that was to be learned in a particular trial. In this particular

trial, the traffic cone presented to participants was located at (25.96, 13.08). The red dot illustrates the small object model (the candle, the bottle, the lock or the wood) attached to the top of the traffic cones, the function of which was to increase the distinctiveness of each traffic cone. For the purpose of illustration, the other three traffic cones and their corresponding objects were also depicted, though they were not seen by participants in this particular trial. The light-red triangles illustrated the other not-presented three traffic cones, which were located at (7.69, -21.78), (34.32, -8.24), and (-3.04, -8.29) respectively. The light-red dots represent the three model objects attached to the top of the three traffic cones.

Figure 7. Response errors as a function of condition and experimental phase in Experiment 2. Error bars are ± 1 standard error.

Figure 8. Response errors as a function of condition and experimental phase in Experiment 3. Error bars are ± 1 standard error.

Figure 9. Response errors as a function of condition and experimental phase in Experiment 4. Error bars are ± 1 standard error.

Figure 1

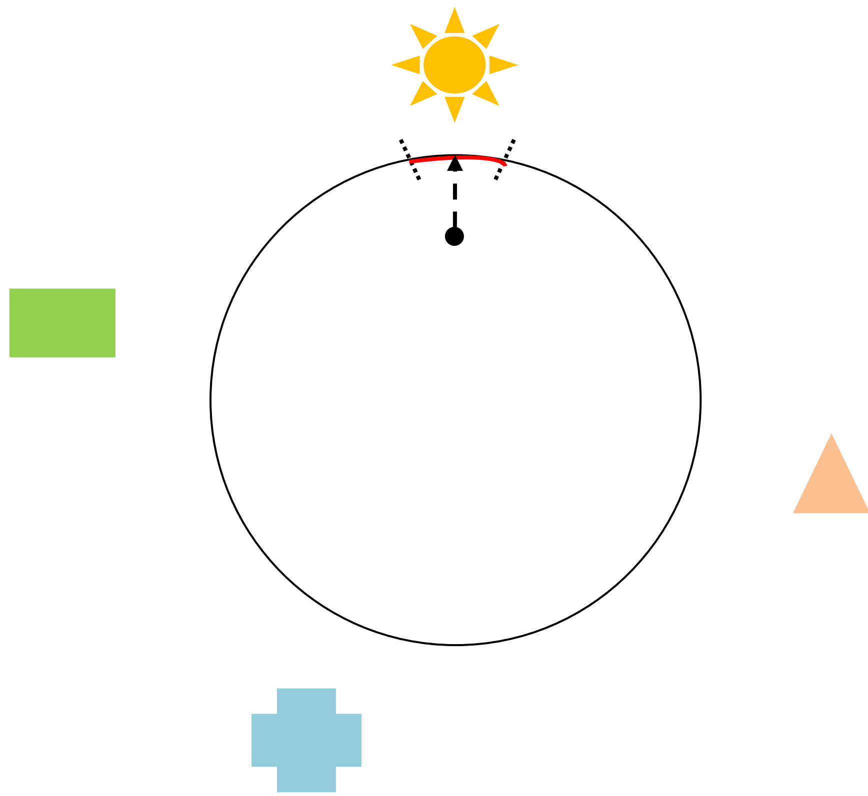
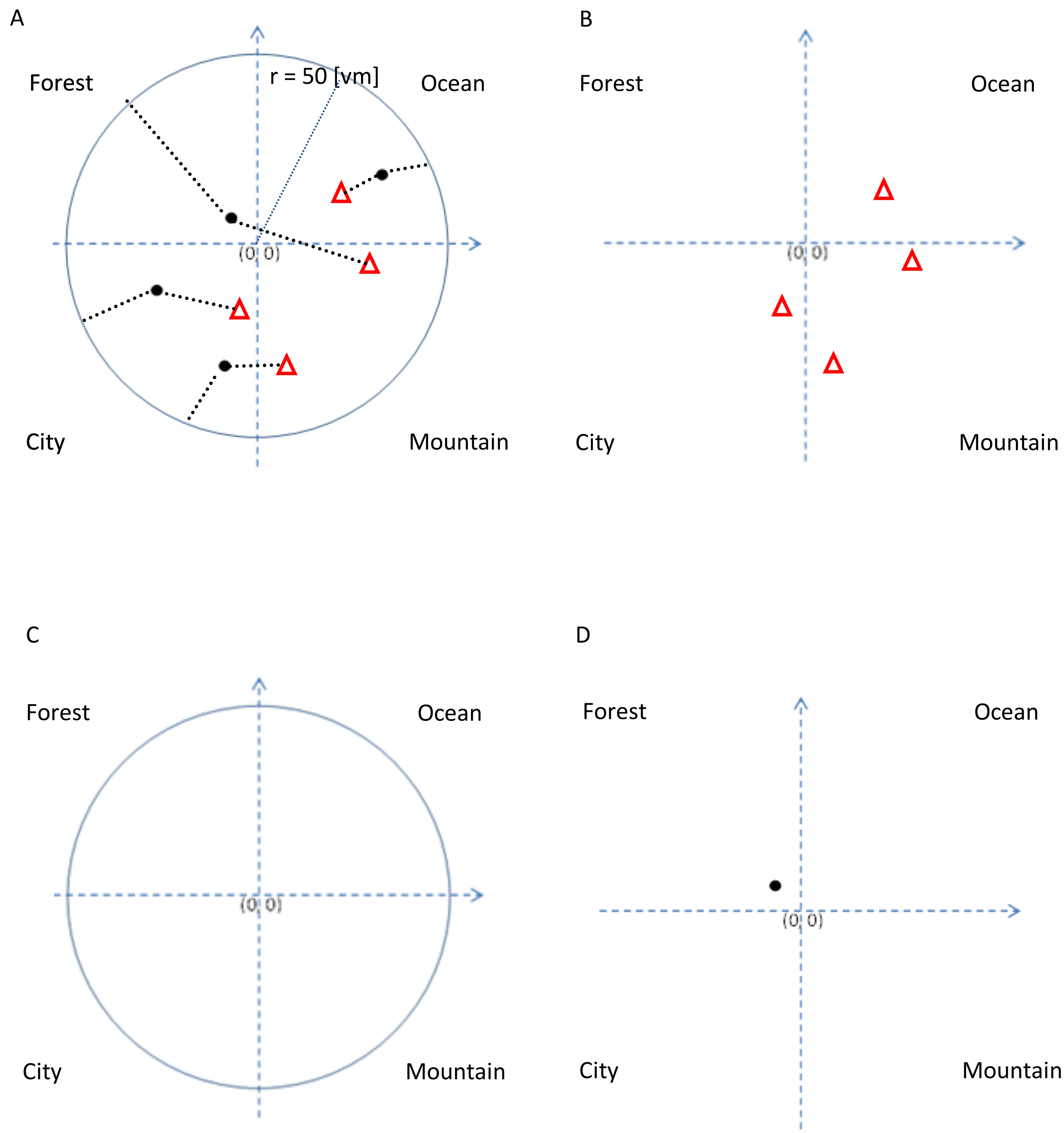


Figure 2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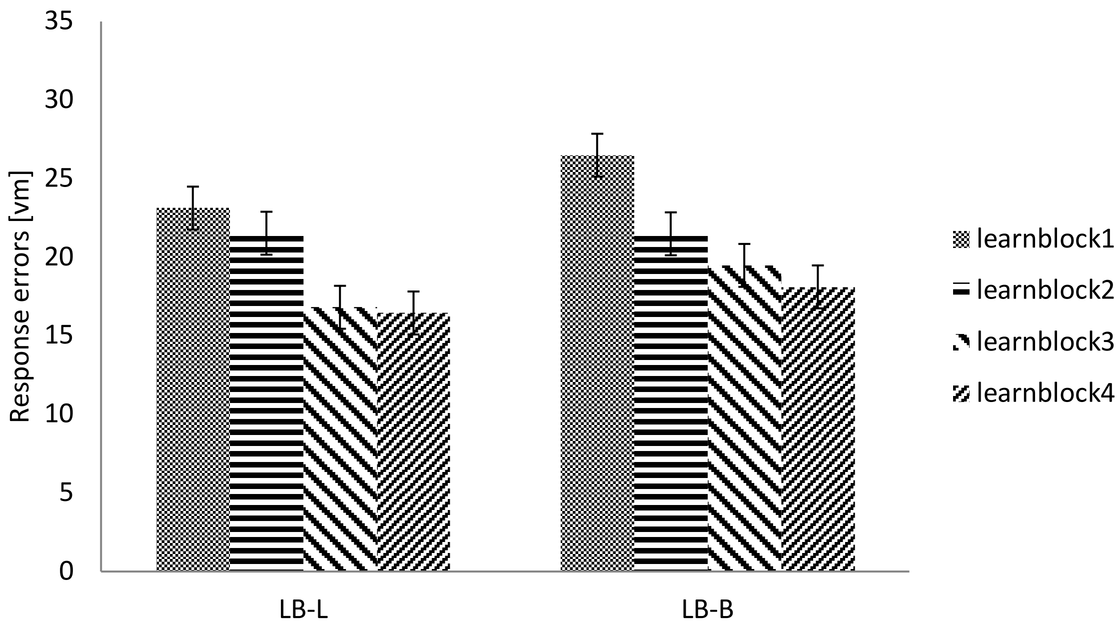
City
Mountain
B
Forest
Ocean
(0, 0)
City
Mountain
C
Forest
Ocean
(0, 0)
City
Mountain
D
Forest
Ocean
(0, 0)
City
Mountain

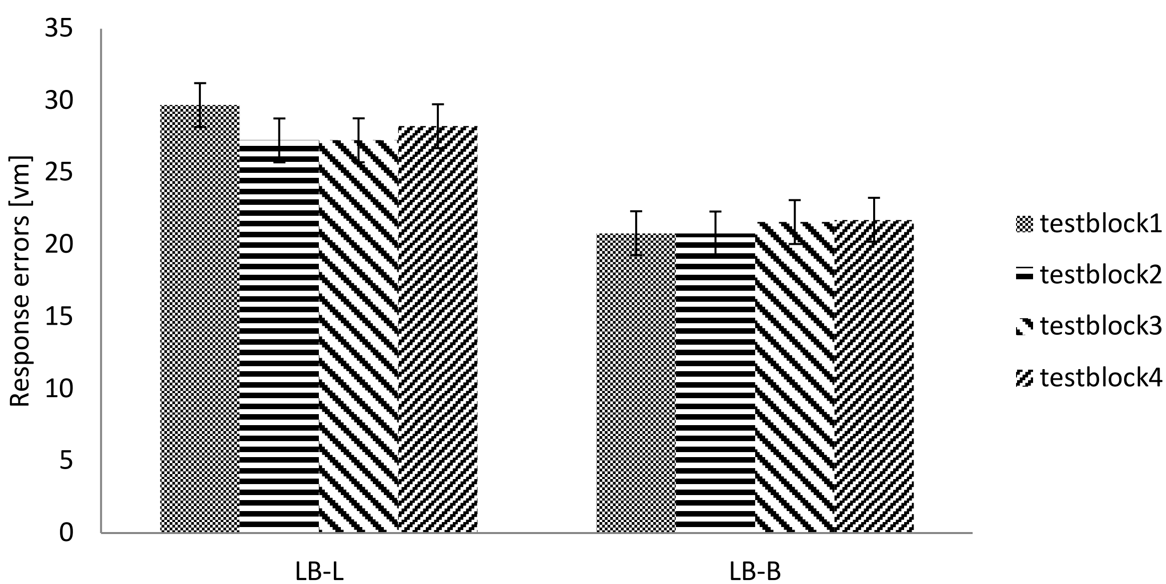
Figure 3

A



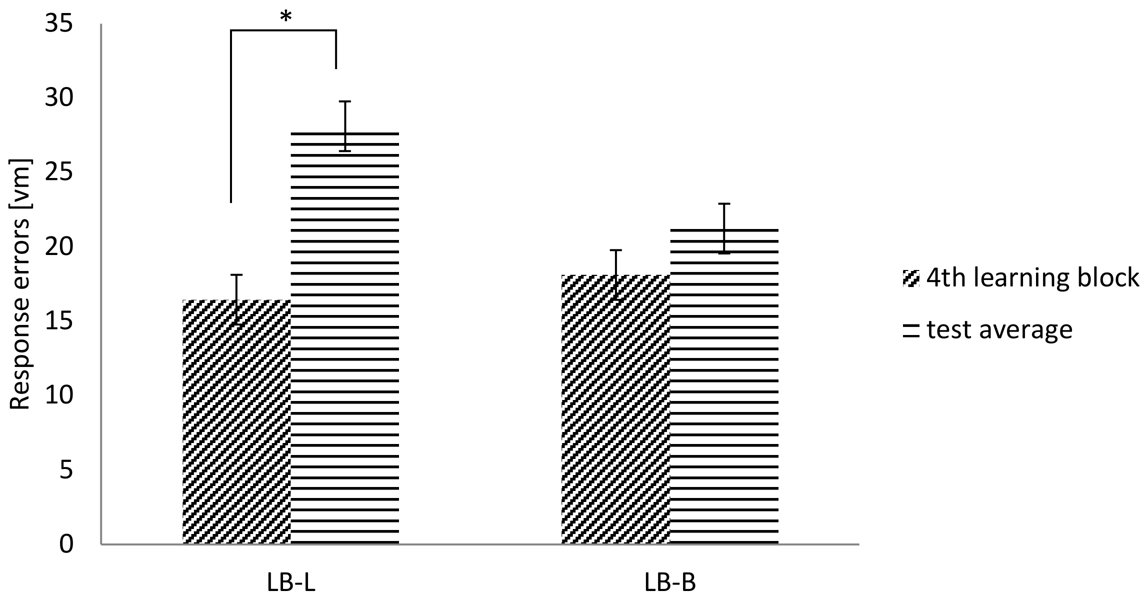
35
30
25
20
15
10
5
0
Response errors [vm]
LB-L
LB-B
learnblock1
learnblock2
learnblock3
learnblock4

B



35
30
25
20
15
10
5
0
Response errors [vm]
LB-L
LB-B
testblock1
testblock2
testblock3
testblock4

Figure 4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30
25
20
15
10
5
0
Response errors [vm]
*
LB-L
LB-B
4th learning block
test average

Figure 5

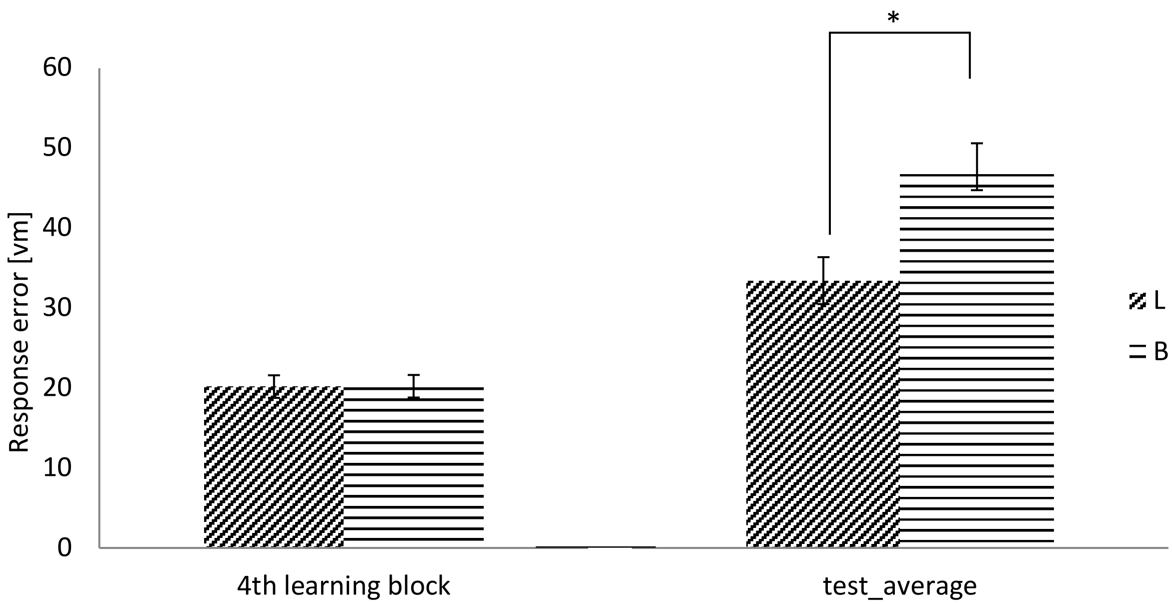
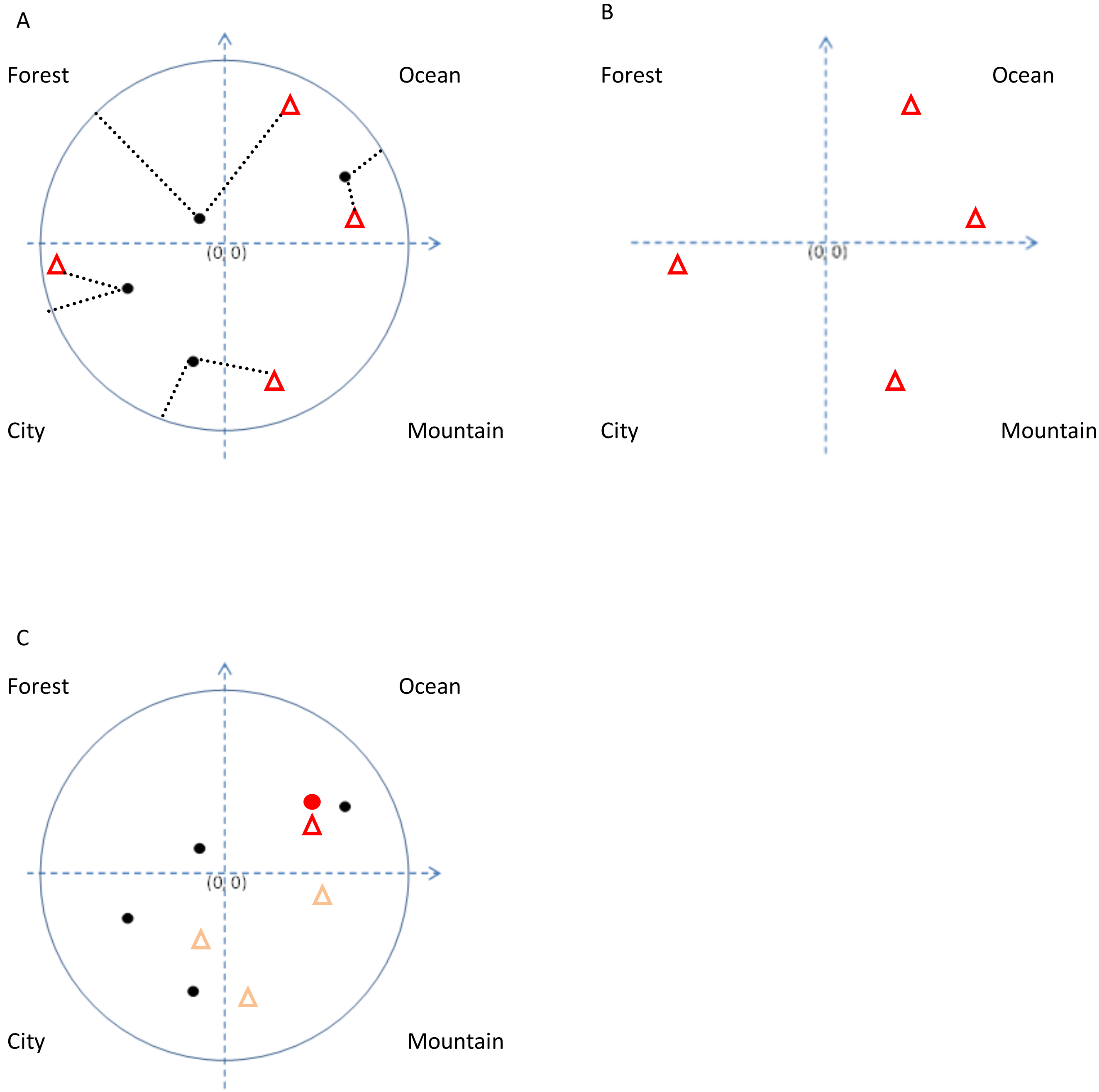

*
60
50
40
30
20
10
0
Response error [vm]
L
B
4th learning block
test_average

Figure 6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Ocean
(0, 0)
City
Mountain
B
Forest
Ocean
(0, 0)
City
Mountain
C
Forest
Ocean
(0, 0)
City
Mountain

Figure 7

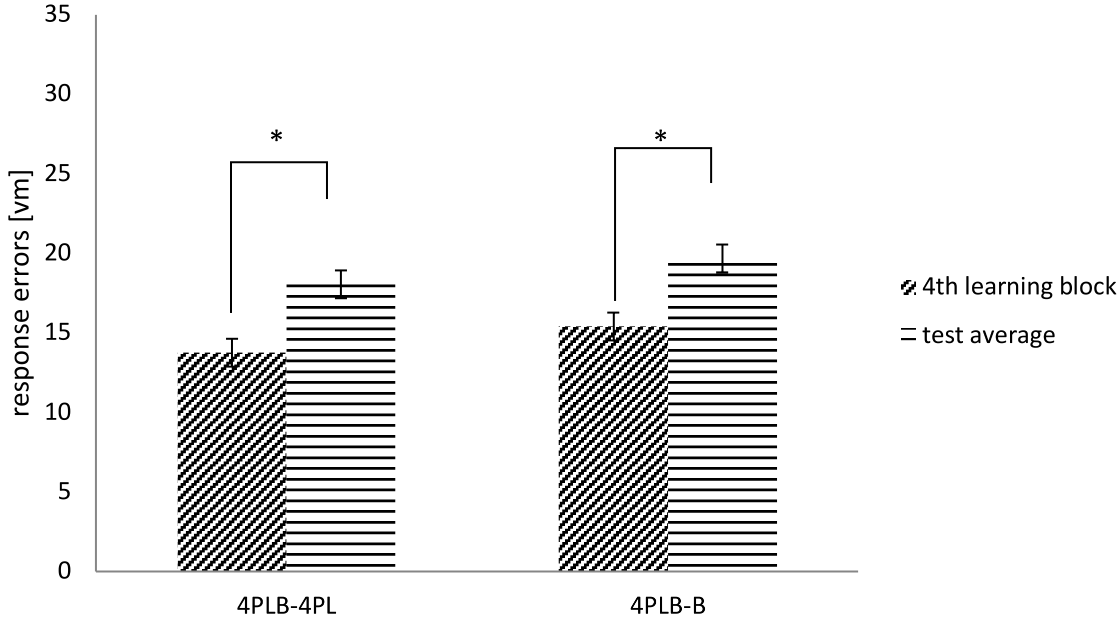

35
30
25
20
15
10
5
0
response errors [vm]
*
*
4PLB-4PL
4PLB-B
4th learning block
test average

Figure 8

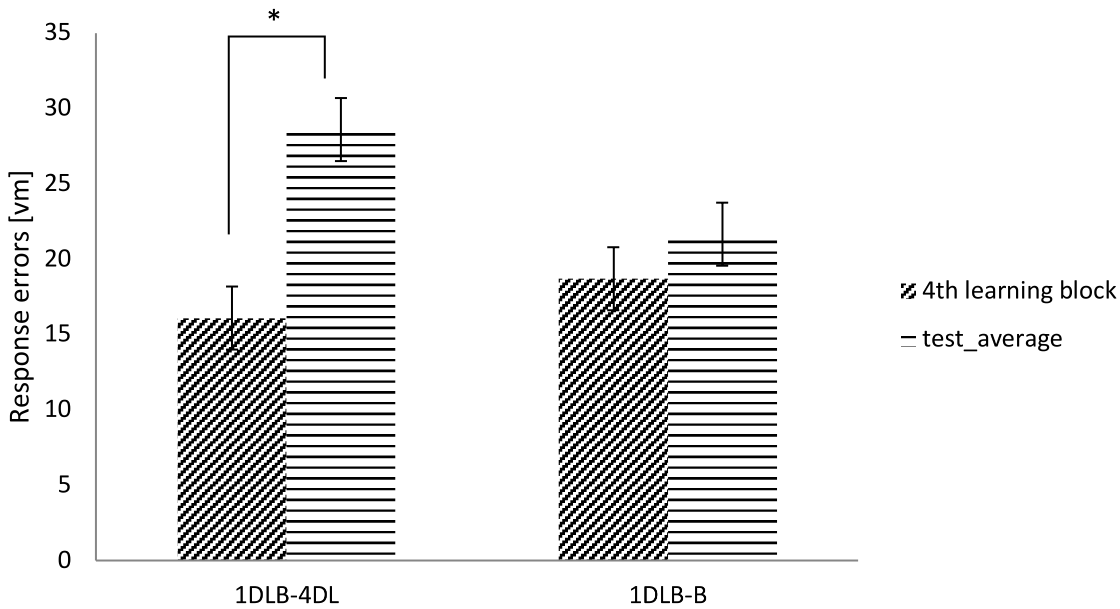
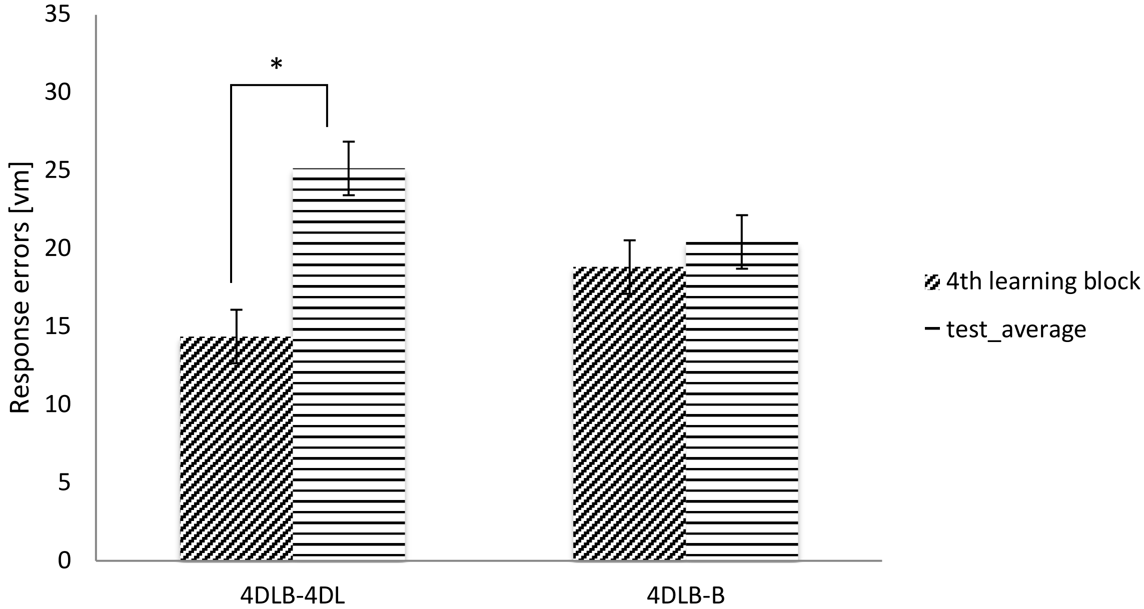

*
35
30
25
20
15
10
5
0
Response errors [vm]
1DLB-4DL
1DLB-B
4th learning block
test_average

Figure 9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30
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20
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10
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0
Response errors [vm]
*
4DLB-4DL
4DLB-B
4th learning block
test_average