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Defining a Boundary in Goal Localization: Infinite Number of Points or Extended Surfaces

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Four experiments examined the roles of extended surfaces and the number of points in the boundary superiority effect in goal localization. Participants learned the locations of 4 objects in the presence of a boundary, landmarks, or both in an immersive virtual environment by reproducing the locations with feedback. Participants then localized the objects in the presence of either the boundary or the landmarks during testing without feedback. The results showed that when both 1 landmark and a circular boundary were presented during learning, localization error during testing increased significantly when only the landmark was presented during testing, whereas localization error did not increase when only the boundary was presented during testing, thus demonstrating a boundary superiority effect. This boundary superiority effect was not observed when 36 landmarks forming a circle and a circular boundary were presented during learning. The landmark superiority effect was observed when 36 landmarks, forming a circular shape, and 1/36th part of the circular boundary were presented during learning. Furthermore, when a varied number of landmarks were presented with a circular boundary during learning, the localization error when the boundary was removed during testing was negatively correlated with the number of the landmarks. These results indicate that the superiority of a circular boundary to a landmark might be due to the larger number of points in the circular boundary but not due to the extended surface of the circular boundary.

Keywords: goal localization, boundary, landmark, spatial memory

Location memory is critical to the survival of humans and animals. When humans and animals rely on location memory, they can retrieve food that they previously stored and can find their way home. A location in an environment can be specified by the visual cues within the environment. Research on spatial memory has distinguished two visual cues, boundary and landmark, within an environment (Burgess, 2008; Lew, 2011). A boundary is an extended surface in the environment and usually separates the local environment from the other environments (e.g., walls of a room). A landmark is a discrete object in the environment (e.g., a tree). A goal location can be specified relative to a boundary in terms of a distance and a direction (e.g., “The goal is one meter north of the south wall”) or to a landmark (e.g., “The goal is one meter south of the tree”).

In addition to a boundary having an extended surface but a landmark does not, a boundary and a landmark differ in at least two other aspects that might lead to difference in encoding a goal location: (a) A boundary has many (or infinite number of) points, whereas a landmark might only act as one point in the environment. An individual point could establish one vector (with a distance and a direction) between it and a goal. More points on a boundary lead to a more precise representation of the goal location. Furthermore, a boundary with many points could form a geometric shape, whereas one landmark acting as a single point is not capable of doing so. When a boundary forms a regular shape (e.g., a circle), the shape itself provides extra information to encode the goal location. For example, the center and the radius of a circle might be used to encode the location of the goal. Hence, a boundary provides a richer frame of reference than a landmark when encoding a goal location due to more individual vectors formed between the points on the boundary and the goal, the global shape formed by a collection of points on the boundary, or both. (b) A boundary is usually stable and relatively distal in the environment, whereas a landmark is usually instable and proximate. A more stable and distal cue might provide more precise encoding of the goal location (e.g., Lew, 2011).

Studies conducted on spatial memory have suggested that the functions of a boundary and a landmark in goal localization depend on two learning mechanisms related to different neural systems. Boundary-based goal localization relies on latent learning through the hippocampus, whereas landmark-based goal localization depends on associative learning through the striatum (Bird, Capponi, King, Doeller, & Burgess, 2010; Doeller & Burgess, 2008; Doeller, King, & Burgess, 2008).

O’Keefe and Nadel (1978) proposed two kinds of spatial memory systems: locale (map) and taxon (route). In the locale system, spatial representations are allocentric and built by latent learning

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(Tolman, 1948). In the taxon system, spatial representations are action based or egocentric and built by learning the association between stimulus and response. The locale system relies on the hippocampus, whereas the taxon system relies on extrahippocampal neural systems. McDonald and White (1994; see also White & McDonald, 2002) empirically demonstrated the distinction between hippocampus-based place learning and striatum-based associative learning. In their study, rats were trained to swim to a visible platform at a constant location in a large circular pool. After training, the rats were able to swim directly to the submerged platform. The rats were then tested with a visible platform in a new location. All the rats with hippocampal lesions swam directly to the visible platform, whereas seven out of the nine rats with striatal lesions swam to the original platform location first and then to the visible platform. These findings indicated that the hippocampus is critical for place learning, whereas the striatum is important for learning the landmark–response association.

With distal landmarks providing orientation cues (Jeffery, 2007), extended boundaries in a local environment might be important distance cues to determine a place within the environment. O'Keefe and Burgess (1996) observed that the location of peak firing of some place cells remained in a constant position relative to the nearest walls when the rats were recorded across environments transformed between a small square, two rectangles, and a large square. O'Keefe and Burgess proposed that the place cells receive inputs from hypothetical boundary vector cells (BVCs) that are tuned to respond to the presence of a barrier or boundary at a given distance along a given allocentric direction (see also Barry et al., 2006; Hartley, Burgess, Lever, & Cacucci, 2000). Hartley, Trinkler, and Burgess (2004) reported that human participants' goal localization in a rectangular virtual-reality room can also be modeled with the input of the vectors from the goal position to the four walls. In contrast, the place cells in rat hippocampi are not tuned to the discrete landmarks within the local environment. Cressant, Muller, and Poucet (1997) reported that the firing field of a given place cell did not change when an array of three discrete landmarks within the environment changed orientation, whereas the orientation of the firing field of the same place cell changed when a card on the boundary was rotated.

Human neuroimaging studies have also revealed the distinctive roles of the hippocampus in boundary-related spatial learning and the striatum in landmark-related spatial learning. Doeller et al. (2008) had participants learn the locations of two targets relative to a landmark and the locations of two other targets relative to a circular boundary in a nonimmersive virtual environment with feedback. The orientation of the environment was presented by distal cues that were presented at infinity. There were four blocks of trials. In each block, participants replaced each object for four times. Across blocks, the relations between the landmark and the boundary changed. Functional magnetic resonance imaging (fMRI) activation of the right dorsal striatum during the feedback phase correlated with the improvement of the goal localization performance for the landmark-related targets, whereas fMRI activation of the right posterior hippocampus during the feedback phase correlated with the improvement of the goal localization performance for the boundary-related targets. Bird et al. (2010) had participants imagine that they were standing in an environment in the presence of horizontally and vertically oriented columns. A horizontally oriented column was conceptualized as a boundary (e.g., a wall) because it extended horizontally and impeded motion across it. A vertically placed column was conceptualized as a landmark. The results showed that fMRI activation of the human hippocampus simply increased with the number of boundaries (i.e., the horizontal columns) but not with the number of discrete landmarks (i.e., the vertical columns).

The latent learning mechanism underlying the boundary-related localization is evidenced by human behavioral studies. Doeller and Burgess (2008; see also Bullens et al., 2010) reported that the presence of a boundary during learning overshadowed the use of a landmark to represent the targets' locations, whereas the presence of a landmark during learning did not overshadow the use of a boundary to represent the targets' locations. This suggests that boundary-related spatial memory might be built through latent learning. However, Wilson and Alexander (2008) reported that previously learning a location relative to a landmark could also slightly impair successively learning a location relative to a boundary, contradicting the proposal that boundary-related learning is latent (Alexander, Wilson, & Wilson, 2009). Since the blocking effect of previously learning a location relative to a boundary on successively learning a location relative to a landmark was much bigger, it still supports the superiority of boundaries to landmarks in localization.

In summary, both human behavioral and neuroimaging studies as well as animal studies have indicated the distinctive roles of boundaries and landmarks in location memory. According to the BVC model (O'Keefe & Burgess, 1996), the distinction between boundaries and landmarks occurs because the hippocampal place cells receive inputs from hypothetical BVCs that are tuned to a boundary but not to discrete landmarks. However, the characteristics that define a boundary and distinguish it from a landmark is not well studied. The BVC model implies that the extended surface of a boundary might distinguish a boundary from a landmark (Bird et al., 2010; Doeller et al., 2008). Doeller et al. (2008, p. 5919) speculated that the influence of a given object on the hippocampal representation of a location might be simply proportional to the horizontal angle subtended by it at the participant, with extended obstacles having a greater influence than discrete ones. Alternatively, Lew (2011) proposed that it might be due to the fact that local landmarks are usually unstable and proximate, and that a boundary is usually stable and relatively distal in the environment. There is growing evidence indicating that a distal landmark in a local environment could be as effective as a boundary in reorientation (e.g., Lew, Gibbons, Murphy, & Bremner, 2010; Ratliff & Newcombe, 2008). However, direct evidence supporting the influence of distance and stability of a landmark in using landmarks as distance cues to goal localization is still required. In fact, it seems that the closer a cue relative is to a target, the more effective the cue is in localizing the target (Hartley et al., 2004).

In this project, we wanted to examine the possibility that an infinite number of reference points in a boundary might differentiate it from a landmark. A boundary has infinite number of points. Although the boundary used in Doeller and Burgess (2008) is circular and essentially featureless, participants might perceptually segment the circular boundary into many evenly sized arcs (e.g., 36 arcs with 10° each). Each arc can be used to establish a vector between it and the target location. This kind of perceptual segmentation is widely used in instrument displays in everyday life (e.g., 12 clocks on a watch). When there are more reference points, more boundary vectors between the reference points and the target are established. Therefore, more BVCs might be activated. The place cell that receives more BVC inputs might have a more precise firing place. Furthermore, the center and radius of the circular boundary in Doeller and Burgess might also be used to encode the location of the goal. Hence, a boundary provides a richer frame of reference so that the boundary-related place representation is more precise than the landmark-related place representation, thus producing the boundary superiority effect.

The current study was designed to investigate whether the extended surface or the larger number of reference points causes the boundary superiority effect in goal localization. In Experiment 1, we replicated the boundary superiority effect reported by Doeller and Burgess (2008) in an immersive virtual environment. As in Doeller and Burgess, participants learned the locations of four targets in the presence of a local landmark, a circular boundary, or both a landmark and a boundary (see Figure 1A). During the test, participants were required to replace the targets at the original locations when only the landmark cue or the boundary cue was present. Therefore, there were four combinations of learning and testing cues: landmark at learning and testing (L-L), landmark and boundary at learning and landmark at testing (LB-L), landmark and boundary at learning and boundary at testing (LB-B), and boundary at learning and testing (B-B). Participants were randomly assigned to one of the four cue groups. Two methods were used to determine the boundary superiority effect. First, as in Doeller and Burgess, the boundary superiority effect was determined by the larger replacement error in LB-L than in L-L but comparable replacement errors in LB-B and B-B, indicating the overshadowing effect of the boundary learning on the landmark learning but not vice versa. Second, the boundary superiority effect

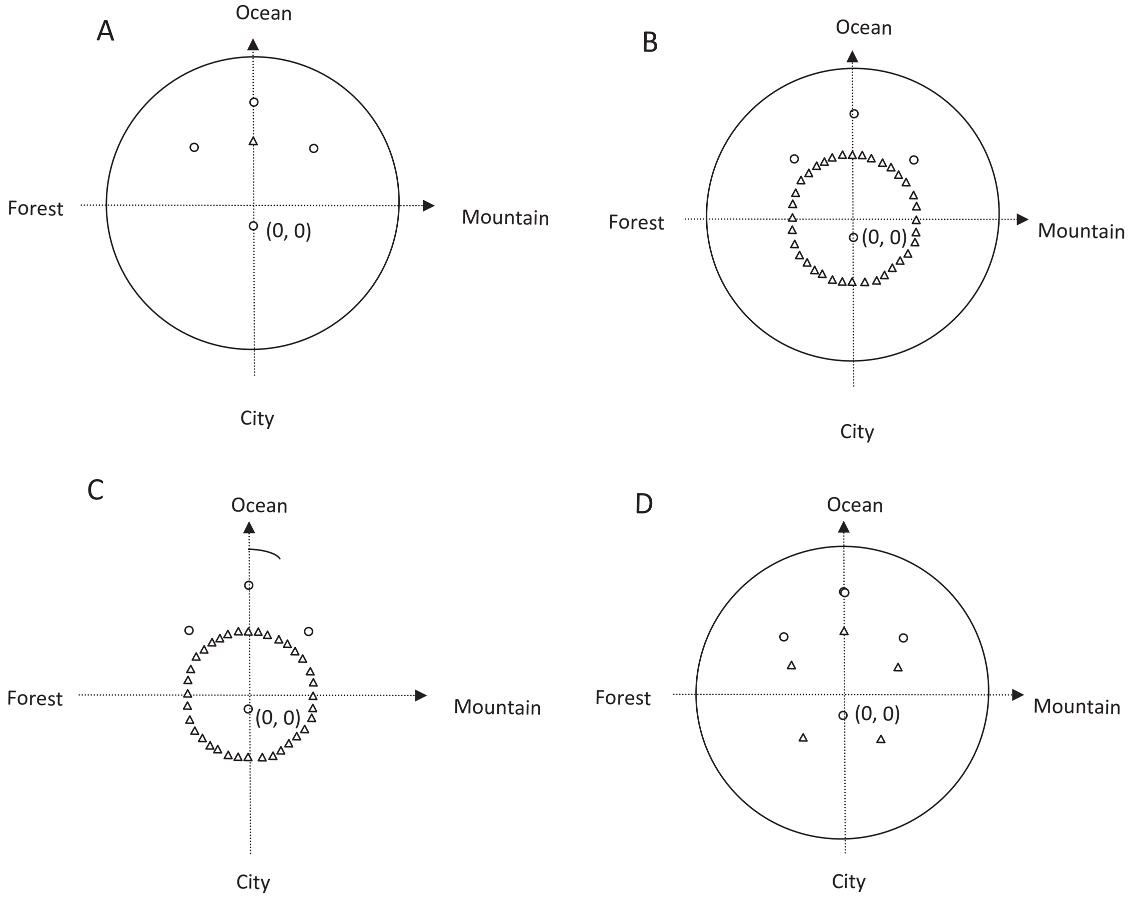

Figure 1. The setting of the experiment environment. (A) The big circle represents the enclosed circular wall. The triangle stands for the traffic cone (landmark), and the four open circles refer to the target locations. The two axes (not shown during the experiment) depict a Cartesian coordinate system that was used to describe to the readers the locations of the items in the environment. One traffic cone and a circular wall were presented in the environment of Experiment 1; 36 traffic cones and a circular wall were presented in the environment of Experiment 2 (B); 36 traffic cones and 1/36th of the circular wall (the arc on the top) were presented in the environment of Experiment 3 (C); and eight numbers of traffic cones (2, 3, 4, 5, 6, 12, 18, and 24) and a circular wall were presented in the environment of Experiment 4 (D). In all conditions, the array of the traffic cones always started at the cone located in Experiment 1 and was evenly distributed around a circle. The condition of five traffic cones was sketched as an example.

was determined by the larger replacement error in the testing blocks than in the learning block in the LB-L group. However, a comparable replacement error across the learning and testing blocks was obtained in the LB-B group, thus indicating that the encoding of the targets' locations relative to the boundary was primary and that the encoding relative to the landmark was secondary or minimal. Encoding of the targets' locations relative to the boundary was primary, so removal of the boundary in the testing blocks in the LB-L group impaired targets' localization substantially. Encoding of the targets' locations relative to the landmark was negligible, so removal of the landmark in the testing blocks in the LB-B group did not impair localization of the targets. It was noted that the second method of determining the superiority effect should be more powerful because the comparison in the second method is within participants, whereas the comparison in the first method is between participants. Hence, in the current study, the second method was primarily used to determine the superiority between landmark and boundary in goal localization.

In Experiment 2, 36 landmarks, forming a circle, replaced one landmark in Experiment 1 (see Figure 1B). The purpose of this experiment was to test whether the boundary superiority effect was eliminated (reduced remarkably) or remained unchanged when the number of the landmarks was increased to 36. If the boundary superiority was caused by the greater number of reference points in a boundary than in a landmark, then the boundary superiority effect should be eliminated or reduced remarkably when there are 36 landmarks. If the boundary superiority was caused by the extended surface in a boundary, then the boundary superiority should remain unchanged, as the 36 discrete landmarks did not contribute to any extended surface (Bird et al., 2010). In particular, the extended surface hypothesis predicts a larger replacement error in the testing blocks than in the learning blocks in the LB-L group as in Experiment 1. In contrast, the reference point hypothesis predicts comparable replacement error across learning and testing or remarkable reduction in the increase of replacement error across learning and testing in the LB-L group compared with Experiment 1. In Experiment 3, a 1/36th section of the circular boundary replaced the circular boundary in Experiment 2 (see Figure 1C). The extended surface hypothesis predicts the boundary superiority effect because the 1/36th part of the circular boundary still has a 10° horizontally extended surface, whereas the 36 discrete landmarks do not contribute to any extended surface beyond the landmarks. In contrast, the reference point hypothesis predicts that landmarks might be superior to the boundary in goal localization. We assume that two reference points with a large angular distance between them provide nonoverlapping localization information and activate different BVCs, whereas two reference points with a small angular distance between them provide redundant localization information and then activate the same BVCs. Hence, the effective reference points in the 36 landmarks might exceed the effective reference points in the 1/36th fraction of the circular boundary. In particular, the reference point hypothesis predicts a larger replacement error in the testing blocks than in the learning blocks in the LB-B group and comparable replacement error across leaning and testing in the LB-L group. In contrast, the extended surface hypothesis predicts a larger replacement error in the testing blocks than in the last learning block in the LB-L group and comparable replacement error across leaning and testing in the LB-B group.

In Experiment 4, only the LB-L condition in Experiment 1 was used. Eight numbers of landmarks (2, 3, 4, 5, 6, 12, 18, and 24) were used across participants. Hence, the linear relationship between the number of landmarks and the increase of replacement error due to the removal of the boundary during testing was directly examined. The reference point hypothesis predicts that the increase in replacement error during testing is negatively correlated to the number of landmarks, whereas the extended surface hypothesis predicts that the increase in replacement error due to removal of the boundary during testing remains constant when the number of the landmark varies.

Experiment 1

The purpose of this study was to replicate the boundary superiority effect by using the paradigm developed by Doeller and Burgess (2008). Participants learned the locations of four objects in a virtual environment in the presence of a landmark, a boundary, or both the landmark and the boundary (see Figure 2). Participants then replaced the targets at their locations in the presence of the boundary or the landmark. The different combinations of cues in the learning phase and the testing phase created four experimental conditions: L-L, LB-L, LB-B, and B-B. In contrast with Doeller and Burgess, in which a desktop virtual environment was used, an immersive virtual environment was used in the current study. In the immersive environment, participants had stereo vision of the virtual environment and changed their orientation in the virtual environment by physically turning their body. In addition, although the virtual environment was conceptually similar to that used in Doeller and Burgess, the three-dimensional models were not completely identical. All these changes required a replication of the boundary superiority effect in the current experimental setting.

Method

Participants. Forty-eight university students (24 men, 24 women) from introductory psychology classes at the University of Alberta participated in this experiment. They received partial course credit for their participation.

Materials and design. The experiment was conducted in a 4 × 4-m room, where the virtual reality systems were located. A swivel chair was placed in the middle of the room. The locations of the items in the virtual environment are depicted with respect to an arbitrarily established Cartesian coordinate system that is illustrated by the horizontal and vertical axes in Figure 1A. Four orientation cues (Ocean, City, Mountain, and Forest) were placed at infinity in each direction of the two coordinate axes (Figure 1A). Functioning as a boundary, a circular wall (1.5 m in height and 50 m in radius) was placed around the origin of the coordinate system. Functioning as a landmark, a traffic cone (1.5 m in height, 0.86 m in width), shown as the triangle in Figure 1A, was placed in the coordinate of (0, 25.46). The four targets (wood, candle, bottle, lock), shown as the four open dots in Figure 1A, were placed at the locations (−19.09, 24.75), (0, 38.18), (19.09, 24.75), (0, −5.66). The association of the objects and the locations were randomized across participants. The sizes of the targets were approximately 0.4 m. The average distance between the targets and the landmarks was 20.51 m. To estimate the distance between the targets and the

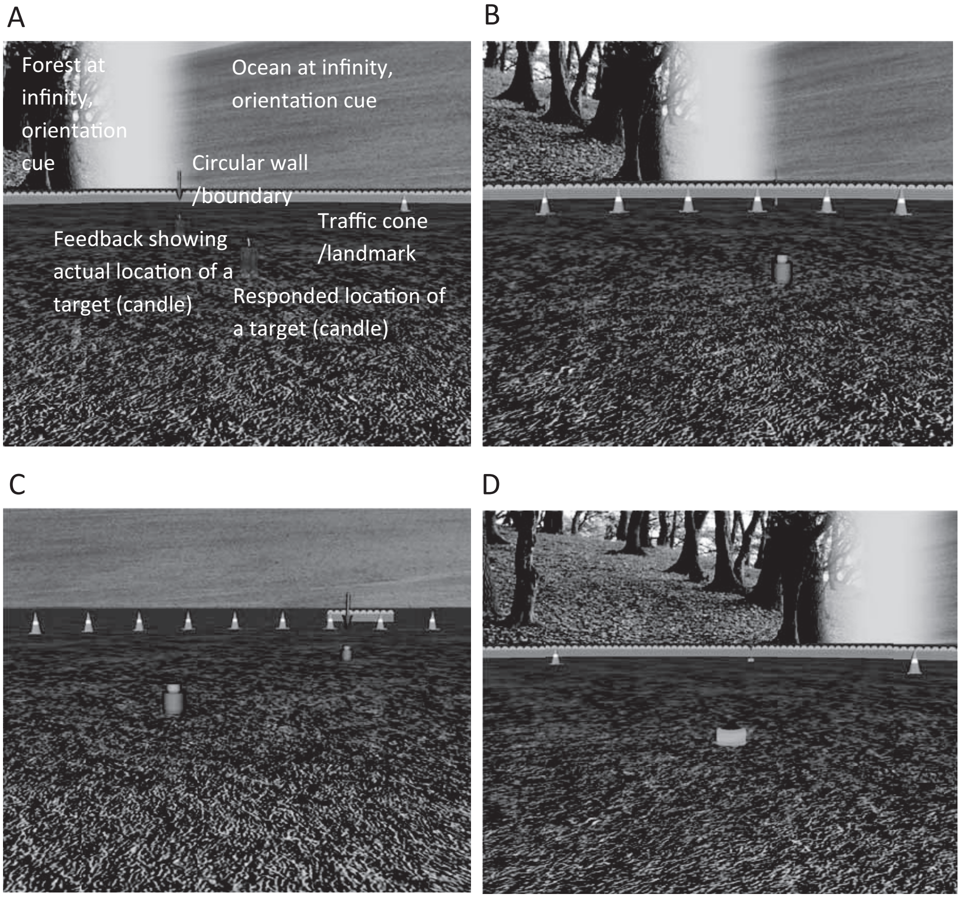

Figure 2. Snapshots of the virtual environment in the learning blocks with feedback. (A) One traffic cone and a circular wall were presented in the environment of Experiment 1. The labels were not presented in the environment and are only used here for exposition Thirty-six traffic cones and a circular wall were presented in the environment of Experiment 2 (B); 36 traffic cones and 1/36th of the circular wall were presented in the environment of Experiment 3 (C); and eight numbers of traffic cones (2, 3, 4, 5, 6, 12, 18, and 24) and a circular wall were presented in the environment of Experiment 4 (D). In all conditions, the array of the traffic cones always started at the cone located in Experiment 1 and was evenly distributed around a circle. The condition of five traffic cones was used as an example.

boundary, 36 points starting from the point (0, 50), which is in the direction of the Ocean in Figure 1A, in 10° steps were selected from the boundary. The average distance between the targets and the 36 points on the boundary was 54.45 m. The distance between the targets and the boundary, and the distance between the targets and the landmarks in all experiments, are listed in Table 1. The distance between the objects and the boundary along the radial line from the 0 point to the boundary was also calculated, as the boundary (with a center and a radius) might be used to encode the distances of the objects from the 0 point (or center). The average distance between the targets and the boundary along the radial line from the 0 point was 23.41 m.

The virtual environment was displayed with an nVisor SX60 head-mounted display (NVIS, Inc., Reston, Virginia). Graphics

Table 1
Average Distances (in Meters) of the Targets Relative to the Boundary and Landmarks in Experiments 1–3 and to the Traffic Cones in Experiment 4

				Experiment 4							
Target relative to	Experiment 1	Experiment 2	Experiment 3	2 cones	3 cones	4 cones	5 cones	6 cones	12 cones	18 cones	24 cones
Boundary	54.45	54.45	32.70	54.45	54.45	54.45	54.45	54.45	54.45	54.45	54.45
Landmark	20.51	35.44	35.44	34.11	35.48	35.62	35.57	35.50	35.43	35.43	35.44

were rendered with Vizard software (WorldViz, Santa Barbara, California). Participants' head orientation was tracked with an InterSense IS-900 motion tracking system (InterSense, Inc., Billerica, Massachusetts). Therefore, the direction of the participants' viewpoint in the virtual environment was determined by participants' head rotation. Participants' viewpoint height in the virtual environment was approximately 1.82 m. Participants used an InterSense wand (a combination of a single hand-held joystick and a 6 DOF tracker) to move forwards and backwards in the environment and to pick up the objects and replace them.

There were three phases in the experiment: initial collection of objects, replacement of objects with feedback (learning), and replacement without feedback (testing). During the initial collection of objects, participants picked up all of the four targets that were visually presented one at a time in a sequence. In the learning and testing phases, participants replaced all of the four targets that were visually probed on the display one at a time in a sequence. There were four learning blocks and four testing blocks, four trials (one for each target) in each block. In the learning blocks, the correct location of each probed object was visually presented after participants replaced the probed object to provide feedback. No feedback was provided in the testing blocks. Participants' initial location and orientation for each trial in the learning and testing blocks was randomized within the circular wall. The association between the objects and the locations was fixed within each participant and randomized across participants.

By presenting cues differently in the learning and test phase, four experimental conditions were formed. Participants would be presented with either both of the two cues (the circular wall and the traffic cone) or one of the cues in the environment during learning. For the compound-cue learning conditions, participants would be tested with only one of the cues presented (LB-L, LB-B). On the other hand, for the single-cue learning conditions, the same cue presented in the learning part was presented in the environment through the test phase (L-L, B-B). Participants were randomly assigned to the four experimental conditions such that each group contained equal numbers of men and women.

There were two independent variables: the cue group (B-B, LB-B, LB-L, L-L), as a between-participants variable, and the replacement block (learning block, testing block). The replaced locations were recorded, and the replacement errors (or distance error), which are the distances between the replaced target locations and the correct target locations, were used as the dependent variable. The distance error was averaged across the four objects in each block for each participant.

Procedure. After participants signed a consent form and read the instructions, they were blindfolded and guided into the experiment room. Participants sat on the swivel chair such that they could rotate themselves when they needed to change their viewpoints in the virtual environment. The participant's attention was first drawn to the circular wall, the traffic cone, and the four orientation cues in the environment, and then they were introduced to using the wand. Participants were told to move toward the four general directions specified by the orientation cues and to familiarize themselves with the environment. Collection of objects started after the participants felt comfortable to proceed with the experiment. In this phase, participants were instructed to pick up the four objects (wood, lock, bottle, and candle; sequence randomized) that are presented in the environment one at a time. After participants collected the four objects, the learning phase followed. In each trial, participants were cued to put each object back to its original location and were then presented with the correct location of the cued object as feedback. Participants were required to collect the target at the correct location. After the learning trials, the testing trials began. In each trial, participants still placed the objects back to the original locations but did not receive any feedback.

Results

As shown in Figure 3A, across the four learning blocks, there was a significant learning effect through feedback, $F(3, 132) = 13.73$, $p < .001$, $\eta_p^2 = .24$. As shown in Figure 3B, across the four testing blocks, there was no learning effect, $F(3, 132) = 1.79$, $p = .153$, $\eta_p^2 = .04$, which was expected, as there was no feedback in the testing blocks. Similar results were observed in the subsequent experiments. Hence, only the replacement error in the last learning block was compared with the replacement error in the testing blocks in this experiment and all subsequent experiments. Distance errors were averaged in the last learning block and in the four testing blocks for each participant. Mean distance error was plotted as a function of the cue group and replacement block (last learning block vs. all testing blocks) in Figure 4.

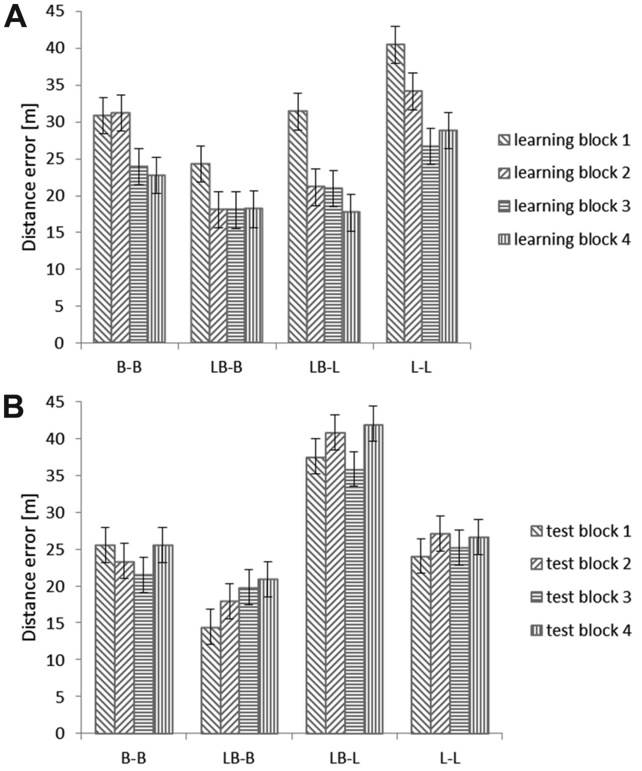

Figure 3. (A) Replacement error as a function of learning block and cue group in Experiment 1. (B) Replacement error as a function of testing block and cue group in Experiment 1. Error bars are ±1 standard error. B-B = boundary at learning and testing; LB-B = landmark and boundary at learning and boundary at testing; LB-L = landmark and boundary at learning and landmark at testing; L-L= landmark at learning and testing.

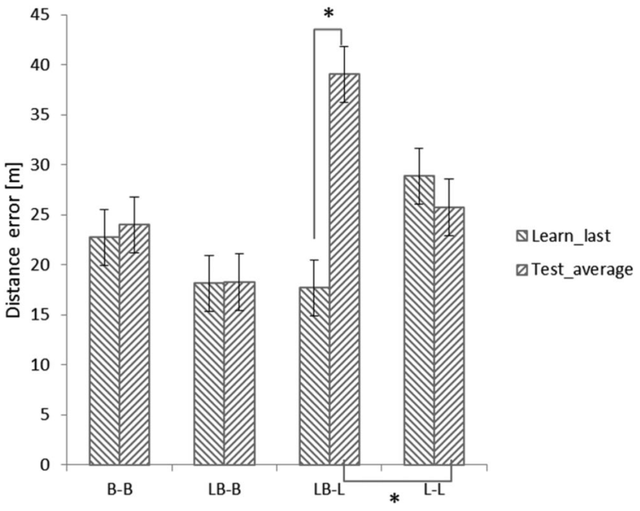

Figure 4. Replacement error as a function of the replacement block (last learning block and all testing blocks combined) and cue group in Experiment 1. Error bars are ±1 standard error. B-B = boundary at learning and testing; LB-B = landmark and boundary at learning and boundary at testing; LB-L = landmark and boundary at learning and landmark at testing; L-L= landmark at learning and testing. Asterisks indicate significance at p level .05.

As illustrated in Figure 4, the replacement error in the testing blocks was larger in the LB-L group than in the L-L group, whereas the replacement error in the testing blocks was comparable in the LB-B group and in the B-B group, thus replicating the overshadowing effect of boundary on learning landmark that was reported by Doeller and Burgess (2008). Furthermore, the replacement error increased in the testing blocks compared with the last learning block in the LB-L condition but not in the LB-B, thus indicating a boundary superiority effect. These two findings were supported statistically.

The replacement error was analyzed in mixed-model analyses of variance (ANOVAs) with variables corresponding to cue group and replacement block. Cue group was between participants, and replacement block was within participants.

The main effect of replacement block was significant, $F(1, 44) = 6.12$, $p = .02$, $\eta_p^2 = .12$. The main effect of cue group was not significant, $F(3, 44) = 1.62$, $p = .20$, $\eta_p^2 = .10$. The interaction between replacement block and cue group was significant, $F(3, 44) = 7.90$, $p < .001$, $\eta_p^2 = .35$. Planned comparisons showed that the replacement error increased significantly in the testing blocks in the LB-L group, $t(44) = 5.39$, $p < .001$, whereas the replacement error did not increase significantly in the testing blocks in the LB-B group, $t(44) = 0.03$, $p = .98$. Planned comparisons showed that the replacement error in the testing blocks was significantly larger in the LB-L group than in the L-L group, $t(44) = 2.27$, $p = .03$, whereas the replacement error did not differ significantly in the LB-B group and in the B-B group, $t(44) = 0.98$, $p = .33$.

Discussion

Experiment 1 replicated the overshadowing effect of boundary on learning a single landmark that was demonstrated by Doeller and Burgess (2008), in spite of the immersive environment used in the current experiment compared with the desktop virtual environment used in theirs. Furthermore, removal of the boundary during testing in the LB-L group remarkably impaired localization performance, whereas removal of the landmark during testing in the LB-B group did not impair localization performance. These results indicate that the targets were primarily represented relative to the boundary and the encoding of targets with respect to the landmark was negligible. Since the overshadowing effect was based on a between-participants comparison, whereas the impairment effect of removing a cue (i.e., boundary or landmark) on the increase of replacement error in the testing blocks was based on a within-participants comparison, the impairment effect should be easier to detect than the overshadowing effect used in Doeller and Burgess. We acknowledge that using the impairment effect to diagnose the boundary superiority effect requires an assumption that cuing efficacy of the boundary and the landmarks does not decrease at different rates over time across learning and test, whereas the overshadowing effect does not require this assumption.[1] However, using the overshadowing effect to diagnose the boundary superiority effect requires an assumption that performance in the last learning block should be the same across different cue conditions (e.g., LB-L and L-L). Otherwise, the difference or no difference in performance on test blocks across cue conditions will be difficult to explain. In contrast, the impairment effect does not require this assumption. Hence, in the subsequent experiments, we primarily examined the impairment effect of removing a cue on the increase of replacement error in the testing blocks to diagnose the boundary superiority effect.

Experiment 2

The purpose of this experiment was to examine whether the boundary superiority effect was eliminated or considerably reduced when the number of landmarks substantially increased. Thirty-six traffic cones forming a circle (equal distance between two adjacent traffic cones, 4.44 m) were used such that there was one landmark in any direction starting from the original traffic cone in Experiment 1 in steps of 10° (see Figure 1B). The reference point hypothesis predicts that the boundary superiority effect is eliminated or greatly reduced, whereas the extended surface hypothesis predicts that the boundary superiority effect remains the same, as the 36 traffic cones do not form any extended surfaces (Bird et al., 2010).

Method

Participants. Forty-eight university students (24 men, 24 women) from introductory psychology classes at the University of Alberta participated in this experiment. They received partial course credit for their participation.

Materials, design, and procedure. The materials, design, and procedure were similar to those in Experiment 1 except that 36 traffic cones forming a circular shape replaced the single traffic cone in Experiment 1. The traffic cone array and the circular wall

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[1] We are grateful to an anonymous reviewer for this suggestion.

shared the same center (see Figure 1B). Thirty-five copies of the original traffic cone (0, 25.46) in Experiment 1 were made by rotating it in steps of 10° around the origin of the circular wall to create the traffic cone array.

Results and Discussion

The mean distance error was plotted as function of cue group and replacement block (last learning block vs. all testing blocks) in Figure 5. The replacement error was analyzed in mixed-model ANOVAs with variables corresponding to cue group and replacement block. The cue group was between participants, and replacement block was within participants.

Neither the main effect of replacement block, $F(1, 44) = 2.39$, $p > .05$, $\eta_p^2 = .05$, nor that of cue group, $F(1, 44) = 0.53$, $p > .05$, $\eta_p^2 = .04$, was significant. Nor was the interaction between replacement block and cue group significant, $F(3, 44) = 0.66$, $p > .05$, $\eta_p^2 = .04$.

Planned comparisons showed that replacement error did not increase significantly in the testing blocks in either the LB-L group, $t(44) = 1.73$, $p = .09$, or the LB-B group, $t(44) = 0.59$, $p = .56$. Hence, no impairment effect was observed. Planned comparisons showed that replacement error in the testing blocks error did not differ significantly in the LB-L and L-L groups, $t(44) = 0.28$, $p = .78$, and did not differ significantly in the LB-B and B-B groups, $t(44) = 0.34$, $p = .74$. Hence, no overshadowing effect was observed.

These results indicated that the boundary superiority effect was eliminated when there were 36 traffic cones. These results were more consistent with the reference point hypothesis than the extended surface hypothesis.

Experiment 3

The purpose of this experiment was to demonstrate a landmark superiority effect on goal localization. One 36th of the circular boundary replaced the circular boundary in Experiment 2 (see Figure 1C). A larger replacement error in the testing blocks than in the last learning block in the LB-B group and comparable replacement error across the last learning block and the testing blocks in the LB-L group would strongly support the reference point hypothesis and challenge the extended surface hypothesis, because 36 traffic cones do not form an extended surface and 1/36th part of the circular boundary still has 10° (or 8.73 m) horizontally extended surface. We chose 1/36 the size of the boundary that was used in the previous experiments so that the boundary in the previous experiments would be perceived as 36 pieces of the boundary used in this experiment, which corresponded to the change from one traffic cone to 36 traffic cones in the previous experiments.

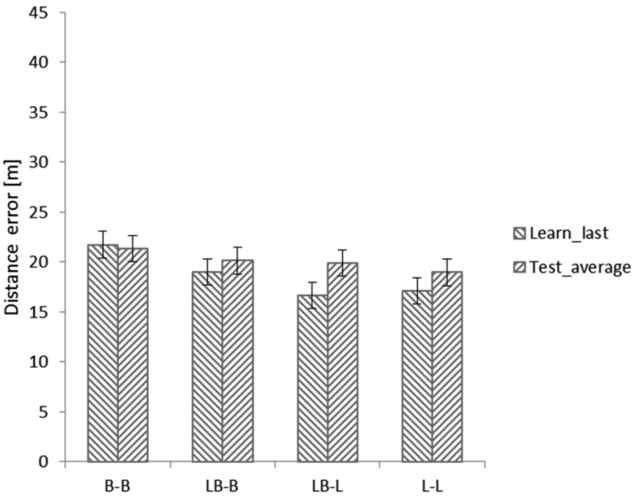

Figure 5. Replacement error as a function of the replacement block (last learning block and all testing blocks combined) and cue group in Experiment 2. Error bars are ±1 standard error. B-B = boundary at learning and testing; LB-B = landmark and boundary at learning and boundary at testing; LB-L = landmark and boundary at learning and landmark at testing; L-L= landmark at learning and testing.

Method

Participants. Forty-eight university students (24 men, 24 women) from introductory psychology classes at the University of Alberta participated in this experiment. They received partial course credit for their participation.

Materials, design, and procedure. The materials, design, and procedure were similar to those in Experiment 2 except that only 1/36th fraction of the circular wall was presented in the current experiment. The 1/36th fraction of the circular wall in the direction of the Ocean in the previous experiment remained presented, and all other portions were removed (see Figure 1C).

Results and Discussion

The mean distance error was plotted as a function of cue group and replacement block (last learning block vs. all testing blocks) in Figure 6. The replacement error was analyzed in mixed-model ANOVAs with variables corresponding to cue group and replacement block. The cue group was between participants, and replacement block was within participants.

The main effect of replacement block was not significant, $F(1, 44) = 0.95$, $p = .34$, $\eta_p^2 = .02$. The main effect of cue group was significant, $F(3, 44) = 7.62$, $p < .001$, $\eta_p^2 = .34$. The interaction between replacement block and cue group was significant, $F(3, 44) = 3.05$, $p = .04$, $\eta_p^2 = .17$. Planned comparisons showed that the replacement error increased significantly in the testing blocks in the LB-B group, $t(44) = 2.66$, $p = .01$, whereas the replacement error did not increase significantly in the testing blocks in the LB-L group, $t(44) = 1.00$, $p = .32$. Hence, the impairment effect was observed when the landmark was removed at test but not when the boundary was removed at test. Planned comparisons showed that the replacement error in the testing blocks error did not differ significantly in the LB-L group and in the L-L group, $t(44) = 1.50$, $p = .14$, and did not differ significantly in the LB-B group and in the B-B group, $t(44) = 0.93$, $p = .36$. Hence, no overshadowing effect was observed. This null effect might be due to the less power in a between-participants comparison.

These results indicated that removal of the landmark array during testing in the LB-B group remarkably impaired localization performance, whereas removal of the boundary during testing in the LB-L group did not impair localization performance, thus indicating that the targets were primarily represented relative to the

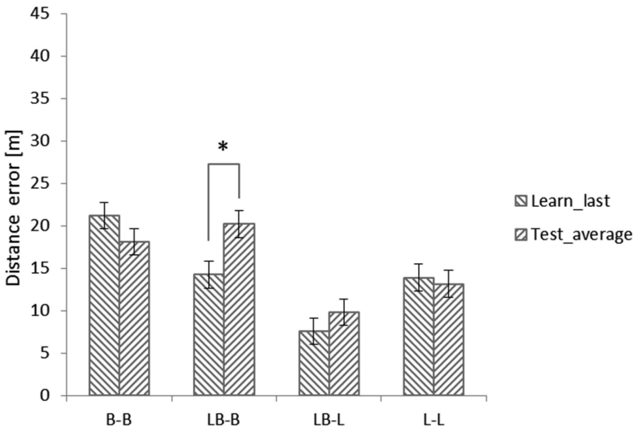

Figure 6. Replacement error as a function of the replacement block (last learning block and all testing blocks combined) and cue group in Experiment 3. Error bars are ±1 standard error. B-B = boundary at learning and testing; LB-B = landmark and boundary at learning and boundary at testing; LB-L = landmark and boundary at learning and landmark at testing; L-L= landmark at learning and testing. Asterisk indicates significance at the *p* level .05.

landmark array and that the encoding of targets with respect to the boundary was negligible. These results strongly support the reference point hypothesis and challenge the extended surface hypothesis.

Experiment 4

Experiment 1, in which there was a single landmark, showed that there was an increase in replacement error when the boundary was removed in the LB-L group, whereas Experiment 2, in which there were 36 landmarks, showed that there was no increase in replacement error when the boundary was removed in the LB-L group. In this experiment, we systematically examined whether the extent of increase in replacement error due to the removal of the boundary is a negative function of the number of the traffic cones before this number increases to a point where there is no replacement error change. Eight numbers of landmarks (2, 3, 4, 5, 6, 12, 18, and 24) were used across participants.

Method

Participants. One hundred forty-four students (72 men, 72 women) from introductory psychology classes at the University of Alberta participated in this experiment. They received partial course credit for their participation.

Materials, design, and procedure. The materials, design, and procedure were similar to those in Experiment 1 except that only the LB-L condition was used and that there were eight numbers of traffic cones (2, 3, 4, 5, 6, 12, 18, and 24) across participants. The different configurations of traffic cone were created by rotating and replicating the original traffic cone in Experiment 1 for the corresponding degree (e.g., for the five-cone configuration, the rotating degree would be 72° such that there was equal distance between two adjacent traffic cones; see Figure 1D). Participants were randomly assigned to the eight traffic cone arrays such that each group contained nine men and nine women.

Results and Discussion

The mean distance error was plotted as a function of traffic cone number and replacement block (last learning block vs. all testing blocks) in Figure 7. The replacement error was analyzed in mixed-model ANOVAs with variables corresponding to traffic cone number and replacement block. The traffic cone number was between participants, and replacement block was within participants.

The main effect of replacement block was significant, $F(1, 136) = 19.54$, $p < .001$, $\eta_p^2 = .13$. The main effect of traffic cone number was marginally significant, $F(7, 136) = 2.03$, $p = .055$, $\eta_p^2 = .10$. The interaction between replacement block and traffic cone number was significant, $F(3, 44) = 2.15$, $p = .04$, $\eta_p^2 = .10$.

The interaction between replacement block and traffic cone number was due to the larger effect of replacement block when the traffic cone number was smaller. To enable us to further examine the linear relationship between the number of cones and the increase in replacement error, the difference of the replacement error across the last learning block and the testing blocks (testing–learning) for each participant was scattered across the number of traffic cones in Figure 8. Three participants (one in the two-cone group and two in the four-cone group) were removed, as their replacement error increases were larger than 100 m, which is the maximum distance in the boundary. The general results did not change regardless of whether the three participants were included in the following analyses. The replacement error increase negatively correlated with the number of the traffic cones (Pearson $R = -.36$, $p < .001$). As illustrated in Figure 8, the predicted replacement error increase at 18 traffic cones was close to 0, which was supported by the statistical analysis. The predicted replacement error increase (2.74 m) at 18 traffic cones did not differ from 0, $t(139) = 1.42$, $p = .16$. We also fit the data with nonlinear models, but did not find a model that could explain remarkably more variance associated with the number of the traffic cones. The best model (a cubic model) could explain 15% of the variance, which was 2% better than the linear model (see Figure 8). Hence, we preferred the linear model for the interest of simplicity.

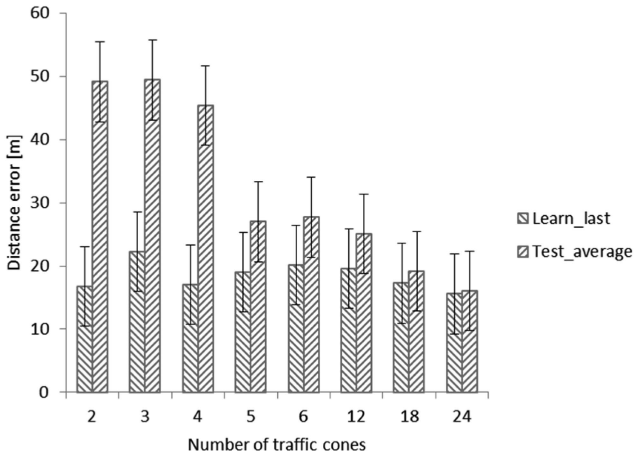

Figure 7. Replacement error as a function of the replacement block (last learning block and all testing blocks combined) and number of landmarks in Experiment 4. Error bars are ±1 standard error.

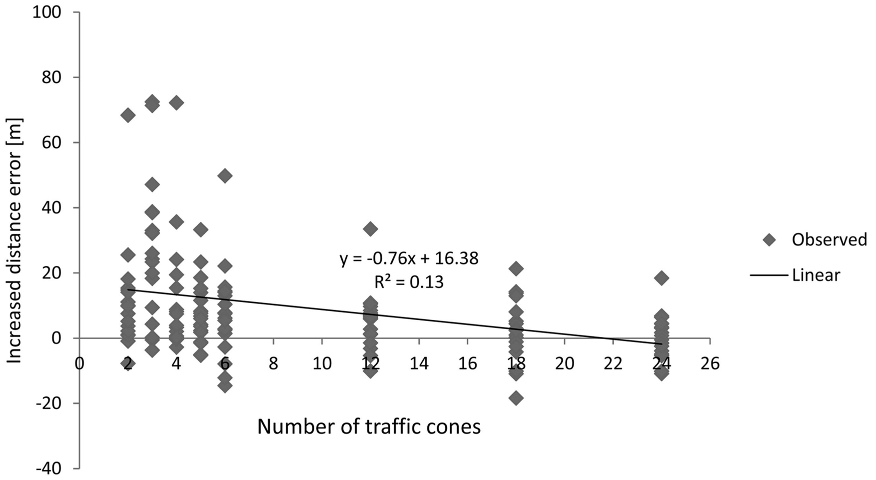

Figure 8. The scatterplot shows the correlation between the replacement error change after the last learning block (Test_average–Learn_last) and the number of traffic cones in Experiment 4. Data were fitted with a linear function.

These results clearly indicated that the removal of the boundary had less impairment in goal localization when there were more landmarks. The linear function indicated that the boundary superiority effect might be eliminated when there were 18 landmarks forming a circular shape. These results support the reference point hypothesis and challenge the extended surface hypothesis.

General Discussion

The experiments in this project were designed to examine whether the extended surface or infinite number of reference points of a boundary differentiates it from a landmark in the organizing of object location memory. The distinctions between a boundary and a landmark in representing object location have been well documented in animal behavioral studies (e.g., McDonald & White, 1994), animal single-cell recalling studies (e.g., Cressant et al., 1997), human behavioral studies (e.g., Doeller & Burgess, 2008), and human neuroimaging studies (e.g., Doeller et al., 2008). The distinction has been explained by the famous BVC model originally proposed by O'Keefe and Burgess (1996). According to the model, place cells receive inputs from hypothetical BVCs that are tuned to respond to the presence of a barrier or boundary at a given distance along a given allocentric direction. A single landmark presumably does not activate BVCs (Bird et al., 2010). However, it is not clear what characteristics of a boundary define a boundary and activate BVCs.

The findings of the current experiments support that a larger number of points, rather than the extended surface of a boundary, defines a boundary or more precisely produces the boundary superiority effect. There are four important findings. First, in Experiment 1, in which participants learned targets' locations with the presence of a circular boundary and a single landmark, the replacement error increased when the boundary was removed but did not increase when the landmark was removed. Second, in Experiment 2, in which participants learned targets' locations with presence of a circular boundary and 36 landmarks forming a circular shape, removal of either the boundary or the landmark array did not impair the targets' replacement accuracy. Third, in Experiment 3, in which participants learned targets' locations with the presence of 1/36th fraction of a circular boundary and 36 landmarks, removal of the landmarks impaired the replacement accuracy but removal of the boundary did not impair the replacement accuracy. Fourth, in Experiment 4, the increase in the replacement error due to removal of the circular boundary after participants learned targets' locations with the presence of both the landmarks and the circular boundary negatively correlated with the number of the landmarks until there was no influence of removal of the boundary.

The first finding indicates that participants primarily encoded the targets' locations with respect to the boundary and that encodings of the targets' locations relative to the landmark were minimal. This boundary superiority effect is consistent with the overshadowing effect in that learning a boundary overshadows learning a landmark but not vice versa, which was originally reported by Doeller and Burgess (2008) using a desktop virtual environment and was replicated in Experiment 1 of the current study with an immersive environment. However, the boundary superiority effect might be due to the extended surface of the boundary or due to the infinite number of the points in the boundary. Doeller et al. (2008, p. 5919) speculated that the influence of a given object on the hippocampal representation of location might be simply proportional to the horizontal angle subtended by it at the participant, with extended obstacles having a greater influence than discrete ones. Hence, a circular wall with a larger extended surface was superior to a discrete landmark in Experiment 1 of the current study. In contrast, a landmark might provide one reference point to encode the location of the target whereas a boundary might provide a larger number of reference points to encode the location of the target. When there are more reference points in a variety of directions, more BVCs might be activated, leading to a more precise place representation. Hence, a circular wall with an infinite number of reference points is superior to a single landmark with a single reference point in Experiment 1 of the current study.

However, the other three findings (from Experiments 2–4) support the reference point hypothesis and challenge the extended surface hypothesis. The findings of Experiment 2 indicate that boundary superiority was eliminated when there were 36 landmarks. The findings of Experiment 3 indicate a landmark superiority effect when there were 36 landmarks and 1/36th fraction of the circular boundary. The findings of Experiment 4 clearly indicate a negative correlation between the boundary superiority effect and the number of the reference points. When the number of the reference points increased to approximately 18, the removal of the circular boundary did not impair target replacement accuracy. These three findings are novel and powerful, as they distinguish between the reference point account and the extended surface account.

These findings are difficult to be explained with the extended surface hypothesis. According to the extended surface hypothesis, an extended surface has greater influence than discrete landmarks in place representation. The number of landmarks should not change the boundary superiority effect when the landmarks do not form horizontally extended surfaces or impede motion across them (Bird et al., 2010). In all these experiments, even when there were 36 traffic cones, the gap between two adjacent cones was 3.65 m, given the 4.4 m between two adjacent cones and the 0.75-m width of a traffic cone, hence the gap did not impair participant movement through it. Therefore, the extended surface hypothesis predicts the boundary superiority effect in Experiments 2–3 and constant boundary superiority effect across number of traffic cones in Experiment 4. However, that was not consistent with the findings of these experiments. In contrast, these findings can be readily explained by the reference point account. According to the reference point hypothesis, a circular boundary has many reference points that could establish many boundary vectors from a target to the reference points, whereas a landmark has one reference point that could establish one boundary vector from a target. Removal of one reference point (the landmark) when there are many others presented should not affect the target localization significantly, whereas removal of all (the boundary) but one reference point should substantially affect the target localization. Furthermore, the center and the radius of the circular shape of the boundary might also be used to encode the location of the target objects. Hence, there is a boundary superiority effect as in Experiment 1. When more landmarks are added to the environment, more vectors can be established between the target and the landmarks. In addition, since the identical objects (i.e., traffic cones) are arranged circularly at constant intervals in the current study, they may form an illusory geometric shape through perceptual organization. The illusory surfaces (or shape) can be more vividly formed as the number of landmarks increases.[2]

Therefore, more accurate representations of the landmark-related target place are developed, leading to a smaller boundary superiority effect as indicated in Experiment 4. When there are enough landmarks, the representation of the target place relative to the landmarks might be as precise as that relative to the boundary, eliminating the boundary superiority effect as indicated in Experiment 2. When the boundary was a fraction (i.e., 1/36th) of a circular wall, there might be fewer reference points on the boundary than on the landmarks. Therefore, a landmark superiority effect might be expected as indicated in Experiment 3.

It was noted that although the boundary was relatively distant from the perspective of the participants standing inside the boundary, the boundary superiority effect was not observed in Experiments 2 and 3. Hence, the findings of the current study indicate that the boundary superiority effect might not occur exclusively because local landmarks are usually proximate and a boundary is usually distal in the environment (e.g., Lew, 2011). Furthermore, according to Table 1, the distance between the landmarks and the targets remained approximately 35 m when the number of the landmarks increased. Hence, the linear change of the replacement error was not due to the distance change between the targets and the landmarks.

The findings of the current study question the speculation that there is a dedicated spatial processing mechanism that is specific for an extended surface but not for an array of objects. It is likely that the BVCs might have taken inputs from the reference points at specific distance and direction whether the reference points were defined by an extended surface or by separated landmarks. Since the BVCs may not be specifically sensitive to an extended surface, the definition of boundary in BVC needs to be refined.

However, Bird et al. (2010) reported that fMRI activation of human hippocampus simply increases with the number of boundaries but does not increase with the number of discrete landmarks, suggesting that BVCs might take extended surfaces but not discrete objects as input. We speculate that in their study there were up to five vertical columns (landmarks) and that fMRI activation of hippocampus might not be sensitive to distinguish whether one or five BVCs were activated. In contrast, for each horizontal column (boundary), there were presumably several reference points. Suppose there are five reference points; adding one horizontal column would add five more reference points and activate five new BVCs, which might significantly change the activation pattern of hippocampus.

The findings of this study have another important implication for the development of the BVC model. To our knowledge, the possible number of boundary vectors for one specific location has not been well determined. Previous studies have indicated that there might be four boundary vectors in a rectangular room (Hartley et al., 2004; O'Keefe & Burgess, 1996). However, it is not clear about the number of the boundary vectors for a given location in a circular boundary. Experiment 4 of the current study provided a method to tackle this issue. The results showed that the boundary superiority effect decreased until it was eliminated as the number of the landmarks increased. The critical number of landmarks at which the boundary superiority effect is removed might indicate the number of boundary vectors for one target in the environment. The linear function (see Figure 8) showed that the boundary superiority effect disappeared when there were approximately 18 landmarks. Due to the explorative nature of Experiment 4, future studies are required to replicate the results. For example, we assumed a linear function between the number of landmarks and boundary superiority effect, and this may not be the best function. Furthermore, the number of landmarks that is required to bring about the boundary superiority effect might depend on multiple factors such as the size of an environment and the size of each landmark.[3] Nevertheless, it is safe to conclude that the boundary vectors for a given location in the environment should be limited, although the number of points on an enclosed boundary is unlimited.

Following the paradigm of Doeller and Burgess (2008), the current study used a circular boundary and an array of landmarks

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[2] We are grateful to an anonymous reviewer for this insight.

[3] We are grateful to an anonymous reviewer for this suggestion.

forming a circular shape. The circular shape was used such that the landmark array and the circular boundary provided distance information and did not provide orientation information. Hence, the findings in the current study are not able to address the distinction between a boundary and a landmark array in reorientation (Gouteux & Spelke, 2001; Lee, Shusterman, & Spelke, 2006; Lew, 2011). It was noted that Kelly, McNamara, Bodenheimer, Carr, and Rieser (2009) reported that spatial orientation relative to surfaces and landmarks was equivalent when other variables (e.g., cue ambiguity) were controlled for. Therefore, it would be interesting to further examine the distinction between boundary and landmarks in different spatial tasks including localization, orientation, and reorientation (Kelly, McNamara, Bodenheimer, Carr, & Rieser, 2008). Furthermore, it is not clear whether the findings of the current study are limited to a circular shape (e.g., Lew et al., 2010; Wilson & Alexander, 2010). Future studies are required to test the reference point account in a variety of shapes of both boundary and landmark array.

In Experiments 2 and 4 of the current study, the landmark array and the circular boundary shared the same center. The results in Experiment 2 indicated that removal of either the boundary or the landmark array did not impair the localization performance. This finding might be attributed to the common center of the boundary and landmark array such that the landmark array and the circular boundary provided completely redundant information to specify the targets' locations. Future studies using different centers are needed to test whether removal of either the boundary or the landmark array will impair the localization performance.

Last but not least, the current project did not examine whether a boundary provides richer reference frames than a landmark to encode a goal location due to more individual vectors between the points on the boundary and the goal, the global shape formed by a collection of points on the boundary, or both. Therefore, further studies are needed to address this issue.

In conclusion, the current study showed several important findings. There was a boundary superiority effect in goal localization when there was a circular boundary and a landmark, whereas there was a landmark superiority effect in goal localization when there were 36 landmarks forming a circular shape and a fraction of the circular boundary. In addition, there was neither a boundary superiority effect nor a landmark superiority effect when there was a circular boundary and 36 landmarks forming a circular shape. Finally, the superiority effect of a boundary decreased as the number of landmarks increased. All these results suggest that the distinction between a landmark and a boundary in goal localization might be attributed to the larger number of points on a boundary than on a landmark, but not due to the extended surface of an enclosed boundary.

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