Boundary Shapes Guide Selection of Reference Points in Goal Localization

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Abstract

This study contrasted two hypotheses theorizing the role of the global shape of a boundary in object location memory. People differentiate reference points based on the global shape extracted from the environment configuration and choose appropriate parts for encoding a specific location. Alternatively, only the number of reference points provided by a shape is important for accurate encoding. We designed a location memory task in an immersive virtual environment to examine the two hypotheses. Participants first learned four target locations with a circular wall and a landmark array. During testing, participants recalled the locations with one entire cue or part of one cue removed. Location memory was impaired when the testing cues did not form a circle, but was not impaired when the testing configuration retained the circular shape. In Experiment 2, the circle formed by a landmark array and the circular wall did not share the same center during learning. Memory performance decreased when either the wall or the landmark array was removed during testing. These results indicated that participants might segment the shape of the circular wall into parts (similar to segmenting a clock face into 12 hours) and encode the target locations relative to the differentiated parts. When such segmentation could be recovered from the testing configuration, object location memory was retained. Otherwise, impairment occurred during testing. These findings suggest that while individual reference points on a boundary are important for encoding specific target locations, the global shape of the boundary affects the segmentation and the selection of individual reference points.

Key words: object location memory, boundary, landmark, cue competition, shape segmentation

Finding a target location is a common and important task that humans and most non-human animals practice daily. Animals must remember where their food has been cached for later retrieval. Human field workers who work outdoors must remember the locations of their home base and working area. The environment in which humans and non-human animals navigate usually contains rich cues that can be used to encode locations in memory and such representations can guide goal localization behavior (e.g., finding a target). Two types of environmental cues have been identified to serve as reference points for goal localization (Doeller & Burgess, 2008; Doeller, King, & Burgess, 2008; for review, see Lew, 2011): a distinctive local landmark (such as a building on campus) or a continuous boundary (such as a wall surrounding a campus).

It has been proposed and empirically demonstrated that encoding a target location relative to a single landmark involves a learning mechanism distinct from that underlying encoding locations relative to a boundary (Bullens et al., 2010; Doeller & Burgess, 2008; Doeller, King, & Burgess, 2008; Bird et al., 2010). In one experiment by Doeller and Burgess, in addition to distal orientation cues, participants remembered four objects' locations with the presence of both a circular boundary and a single landmark within the boundary (compound learning-cue groups) or with the presence of either of these two cues (single learning-cue groups). In the testing phase, the compound learning-cue groups replaced the targets with the boundary alone (the landmark removed) or the landmark alone (the boundary removed). The single learning-cue groups replaced the targets with the presence of the same cue as that during learning. The results showed that when the landmark was presented as the testing cue, less accurate location memory was observed in the compound learning-cue group than in the single learning-cue group. In contrast, when the boundary was presented as the testing cue, comparably accurate location memory was observed in the compound learning-cue group and in the single learning-cue group. These results indicated that boundary-related encoding impaired (overshadowed) landmark-related encoding but not vice versa. The authors concluded that encoding a location relative to a boundary follows the latent/incidental learning rule, whereas encoding a location relative to a single landmark follows the associative learning rule. Doeller, King, and Burgess (2008) further proposed that what makes boundaries different from individual landmarks on the neural computation level is that place cells in the hippocampal system are tuned to a boundary rather than a single landmark.

In a follow-up study of Doeller and Burgess (2008), Mou and Zhou (2013) distinguished two factors that might contribute to the ‘boundaryness’ of a continuous surface: the large number of reference points provided by a boundary or the extended surface. Mou and Zhou hypothesized that the finding that boundary-related encoding overshadowed landmark-related encoding but not vice versa might be attributed to a large number of reference points in a boundary, rather than the extended surface. A continuous boundary contains an infinite number of reference points, which allows vectors from multiple directions to be established between the boundary and a target location. In contrast, a single landmark may provide only one reference point, and thus allows for only one vector between the landmark and a target location. In the experiment of Doeller and Burgess, for the compound learning-cue conditions, when the landmark was removed, only one vector was withdrawn; whereas when the boundary was removed, all vectors but one were withdrawn. Therefore, object location memory decreased in the latter case but was maintained in the former case. Mou and Zhou referred to this hypothesis as the multiple-reference-point hypothesis.

Mou and Zhou (2013) provided empirical evidence supporting the multiple-reference-point hypothesis. Similar to Doeller and Burgess’ paradigm (2008), four conditions were employed in the first experiment of the study: two single-cue conditions where participants learned four objects' locations and were tested subsequently with the same cues, either a circular wall (the boundary condition, referred to as B) or a single traffic cone (the landmark condition, referred to as L); two compound-cue conditions where participants learned with both the boundary and the landmark but were tested with either the circular wall (referred to as BL-B) or the traffic cone (referred to as BL-L). Object location memory was assessed as participants replaced the objects to their remembered locations. Distance errors were recorded, as measured by the distance between a response location and the corresponding correct location. The results showed that larger distance errors in the testing phase than in the learning phase occurred in the BL-L group but not in the other three groups, including the BL-B group. These results indicated that the boundary-related encoding impaired the landmark-related encoding, whereas in the BL-B group the landmark-related encoding did not impair the boundary-related encoding, consistent with the overshadowing effect in Doeller and Burgess. We refer to the larger distance errors in the testing phase than in the learning phase as *the impairment effect*.

Importantly, in the second experiment, Mou and Zhou (2013) replaced the single cone with an array of cones forming a circle, which was concentric with the circular wall. Again, the two compound-cue condition (referred to as BL-L and BL-B, here L refers to the landmark array) and the two single-cue conditions (referred to as L and B) were employed. Strikingly, there was no impairment effect in any of the four groups. In their last experiment, Mou and Zhou systematically manipulated the number of the cones (from two to 24). The results showed that the magnitude of the impairment effect in the BL-L group was negatively correlated with the number of the cones when the array consisted of 12 or less cones; the impairment effect was however eliminated when there were 18 or more traffic cones in the array. Therefore, an array of evenly-spaced cones (e.g. 18 or more cones) could function as a boundary in the sense of no impairment effect upon the removal of the continuous wall at test. Since the array of cones did not have any continuous surface, the large number of reference points rather than the extended surface of a boundary might have caused the findings that boundary-related encoding impaired (overshadowed) landmark-related encoding but not vice versa, supporting the multiple-reference-point hypothesis.

The multiple-reference-point hypothesis can be regarded as an expansion of the Boundary-vector-cell (BVC) model originally proposed by O'Keefe and Burgess (1996; see also Barry et al., 2006; Barry & Burgess, 2014). According to the BVC model, a place cell receives its input from an ensemble of boundary-vector cells that are tuned to barriers (extended surfaces) from multiple directions with a fixed distance to a navigator; the firing rate of the place cell is the thresholded sum of the inputs from the boundary-vector cells (Barry et al., 2006; Barry & Burgess, 2014). According to the multiple-reference-point hypothesis, the accuracy of location memory increases with the number of reference points. Therefore, these two models are essentially similar except that the multiple-reference-point hypothesis stipulates that the vectors to the target can be originated from not only extended surfaces but also discrete objects. The multiple-reference-point hypothesis is also similar to the vector-sum model proposed by Cheng (1988, 1989) to explain how pigeons use landmarks to find a location (see also the multiple-bearings hypothesis for nutcrackers' caching behavior, Kamil & Cheng, 2001). According to the vector-sum model, pigeons record a number of "landmark-to-goal" vectors from the goal position and these vectors contain both distance and directional information. Furthermore, these vectors are assigned with different weightings, with larger weightings to the closer landmarks, as reflected by the observation that shifting the positions of different landmarks exerted controls to different degrees on pigeons' searching locations for the same target (Cheng, 1989).

All the three models discussed above give credit to the individual vectors established between multiple reference points and a target location. However, according to these models, the global shape formed by the multiple reference points might not be critical in the localization process. In particular, in Mou and Zhou (2013), participants might encode one target location relative to all the reference points available during learning. The accuracy of location memory during testing would not decrease as long as there were enough reference points (e.g. 18 or more cones) available at retrieval. When the number of the reference points at retrieval was not sufficient, the accuracy of object location memory decreased linearly with the decrease in the number of the cones presented during testing. We refer to this stipulation as the sufficient-reference-points hypothesis as it only regards the number of reference points at retrieval as the determinant for accuracy in location memory. Below, we will propose an alternative account that also emphasizes the role of the global shape information derived from the configuration of multiple reference points.

Although the function of global shapes in goal localization is less investigated, the function of global shapes in reorientation has been prevalently reported (see Cheng & Newcombe, 2005 for a review). In his seminal work, Cheng (1986) trained rats to find food located at one of the four corners in a rectangular enclosure after disorientation. Despite that the enclosure contained highly informative featural information (such as distinctive panels at each corner), rats seemed to rely on the global geometry of the enclosure (i.e. the rectangular shape) to reorient themselves: they mainly searched at the correct corner as well as at its diagonal opposite, which is geometrically identical to the correct corner, but failed to distinguished the two by the unique features available at the corners. Since this original observation, the reorientation paradigm has been widely employed to test various species in different environmental settings (Vallortigara, Zanforlin & Pasti, 1990; Kelly, Spetch & Heth, 1998; Sovrano, Bisazza & Vallortigara, 2002; Hermer & Spelke, 1994; for reviews see Cheng, Huttenlocher, & Newcombe, 2013). Although early reorientation research has started a debate on the universal dominance of geometric information in controlling the reorientation process across species (e.g., Cheng, Huttenlocher, & Newcombe, 2013; Lee & Spelke, 2010; Lew, 2011; Learmonth, Nadel & Newcombe, 2002), growing evidence from the last decade suggests that boundary primacy is not always observed. Studies using rats (e.g., Pearce et al., 2006) as well as humans (e.g., **Buckley, Smith, & Haselgrove, 2019**) have demonstrated that learning of geometric shape imposed by a boundary can be interfered by learning of non-geometric cues (e.g., overshadowing and blocking).

Extending the important role of global shapes in reorientation, we propose a shape-based segmentation model that acknowledges the importance of the global shape of a boundary in goal localization, especially in selecting the reference points from the boundary to encode target locations. According to the model, people first segment a boundary based on the shape of the boundary. If the shape of the boundary indicates a clear orientation, for example, an isosceles triangle, then the reference points on the boundary can be differentiated based on the shape itself. If the shape of the boundary does not indicate a clear orientation, for example, a circle, then the reference points on the boundary is differentiated based on the distal orientation cues (e.g. Doeller & Burgess, 2008) or based on inertial locomotion cues (e.g. Foo, Warren, Duchon & Tarr, 2005; Yoder, Clark & Taube, 2011). After the segmentation, people specify the location of a target relative to one or several differentiated local segments (i.e. segments that are closer to the target) by establishing vectors between the segments and the target. For instance, to specify the location of a target in a square room, one could divide the room into four corners and four walls. Using orientation information available in the room, which could be originated from a distal landmark or from inertial locomotion, one could distinguish the four otherwise identical corners and the walls. One could then choose a differentiated corner or a wall as a reference point for encoding the target location. We refer to this model as the shape-segment hypothesis. The shape-segment process is in line with the ideas of differentiating locally similar corners based on a global shape (Miller & Shettleworth, 2007).

We contrast the shape-segment hypothesis with the sufficient-reference-points hypothesis using the findings in Mou and Zhou (2013). As illustrated in Figure 1A, three of the four targets were outside the circular cone array but were inside the wall in the study. The other target was inside both circles. The results showed that the impairment effect (i.e. the larger distance error during testing than during learning) due to the removal of the wall during testing was negatively correlated with the number of the cones when this number was below 12; the impairment effect was eliminated when there were 18 or more cones. The shape-segment hypothesis could well explain these findings. According to this hypothesis, participants may divide the wall into equal segments/edges. This process is analogous to dividing the boundary of a clock into different hours (See Figure 1A). Participants then differentiated the segments by using the orientation cues. This is similar to labeling each hour by numbers (e.g., 12 o'clock). The location of a target was then encoded primarily relative to the closest segments. For example, the target location on the Ocean side (shown as the dot closest to the Ocean direction in Figure 1A) can be specified by establishing a vector between the specific location and the wall segment pointing to the Ocean direction (e.g. 11.82 meters inside the Ocean segment of the wall). When participants perceived the circle formed by the cones (18 or more cones), they also segmented this circular array and encoded a target location relative to the edge of the circle formed by the cones (e.g. the target location closest to the Ocean direction in Figure 1A was 12.72 meters outside the Ocean segment of the cone array).

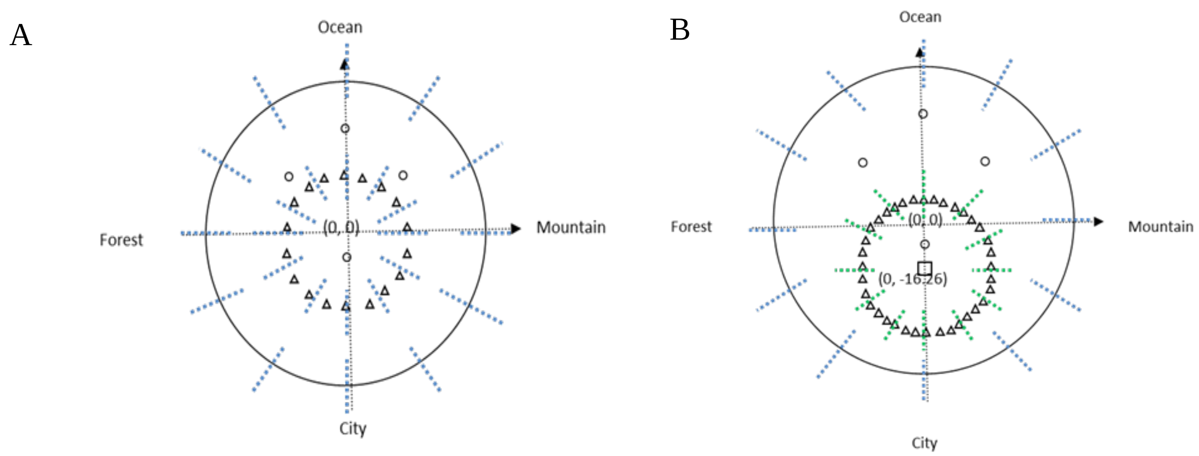


Figure 1. Schematic diagram of the segmentations based on the global shape of the environmental cues. The proposed environment segmentations are based on a circular wall (depicted as the circle) and a landmark array of multiple evenly-spaced cones (depicted as the triangles). A represents segmentations when the circular wall and the circular cone array shared the same center, as marked by the coordinate (0, 0). The dashed blue lines illustrate the hypothetical segmentations based on the two circles. The four target locations are depicted as the four dots. The four labels, Ocean, Mountain, City and Forest, illustrate the distal orientation cues. B represents segmentations when the circular wall and the cone array are eccentric: the wall is centered at (0, 0), whereas the cone array is centered at (0, -16.26) (depicted as the square). The blue dashed lines illustrate the segmentation of the environment based on the wall

cue, whereas the green dashed lines illustrate the segmentation of the environment based on the array cue.

It is important to note that the wall and the circle formed by the cone array shared the same center in Mou and Zhou's study (2013). Therefore, the segments of the two circles were completely aligned (illustrated as the blue dashed lines in Figure 1A). In particular, the distance between the corresponding local segments (segments in the same allocentric direction, e.g. the Ocean direction) of the two circles was the same across different directions. Specifically, the distance was equal to the radius difference between these two circles. If participants remember the distance from a target to the edge of one circle, they should be able to easily calculate the distance from the same target to the corresponding edge of the other circle. For the target inside both circles, its distance to the wall edge minus its distance to the edge of the cone array was the radius difference. For the other three targets outside the cone array and inside the wall, the sum of the two distances was the radius difference.

Consequently, the vectors from one target to the edges of either circle can be computed based on the vectors from the same target to the edges of the other circle. Therefore, the removal of the wall should not affect location memory if participants perceived the circle formed by the cones. With the decrease in the number of the cones (e.g. from 18 to 2), participants were less likely to perceive the circular shape of the cone array, thus the cones were more likely to be treated as separate landmarks (discrete reference points). Lack of the segmentation information therefore led to the impairment effect in testing. Therefore, the impairment effect due to the removal of the wall was observed and the magnitude of such effect increased when the number of the cones decreased. In addition, previous research has shown that the relative salience of discrete landmark cues and boundary cues has impact in determining the attention resources devoted to the landmark/boundary and hence, modulates the associative strength of the cue for learning (e.g., Buckley, Smith & Haselgrove, 2015; Kosaki, Austen, & McGregor, 2013). As a circular shape might be intrinsically more salient than discrete landmarks, participants were more likely to use the wall instead of the separate cones to specify the targets' locations during learning.

The sufficient-reference-points hypothesis can also explain the findings in Mou and Zhou's study as long as we assume that the accuracy of object location memory would not decrease if there were at least 18 reference points available to the participants during testing regardless of the configuration formed by these reference points; otherwise, the accuracy of replacement performance decreased linearly when the number of the reference points (i.e. the cones) decreased.

In summary, the sufficient-reference-points hypothesis stipulates that the number of individual vectors is solely critical to accurate remembering of target locations, whereas the shape-segment hypothesis stipulates that the global shape information obtained from the configuration of the reference points is also important. As the previous studies could not distinguish between these two hypotheses empirically, we distinguished between them in the current study.

In Experiment 1, we manipulated the configurations of the environmental cues, whether forming an enclosure or not, while keeping the same number of reference points during testing. According to the sufficient-reference-points hypothesis, the number of individual reference points alone is critical to accurate recall of target locations. Therefore, we would not expect any effect from removing the global shape of the reference points as long as a sufficient number of reference points remain during tests. According to the shape-segment hypothesis, breaking the integrity of the shape information during testing will impair the segmentation information available to participants, thus impeding their accuracy in remembering during test.

In Experiment 2, we moved the center of the cone array so that the circle formed by the cones and the wall did not share the same center in the learning phrase. Either one of the circles was removed during the testing phase. According to the sufficient-reference-points hypothesis, the number of individual reference points is critical to accurate encoding and recall of target locations. Therefore, we would not expect any impairment effect of removing either circle, as the remaining circle should provide a sufficient number of reference points. In contrast, according to the shape-segment hypothesis, the two eccentric circles would result in two different and independent segmentations as the local edges from these two circles are not aligned (see Figure 1B). Therefore, after learning the target locations respective to the two eccentric circular boundaries, participants would show an impaired memory for object locations during testing when either circle is removed.

Experiment 1

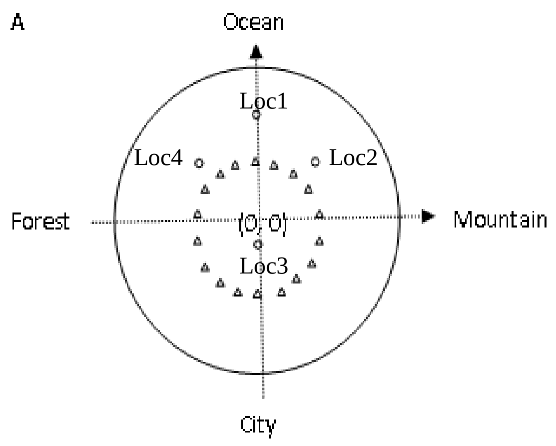
The purpose of Experiment 1 was to examine whether environmental cues that provide an adequate number of reference points alone would be sufficient to eliminate the impairment effect due to the removal of the wall in remembering goal locations. Alternatively, an enclosure and enough reference points may both be necessary to eliminate the impairment effect due to the removal of the wall in remembering goal locations. The sufficient-reference-points hypothesis predicts the former, whereas the shape-segment hypothesis predicts the latter.

Four conditions were used to test these two possibilities. The purpose of the first condition was to replicate the previous finding that a landmark array of 18 evenly spaced cones could function as a boundary-like cue in encoding and subsequent remembering of object locations. We referred to this condition as ConeCirc-ConeCirc (standing for the “circular cone array” used in both the learning and testing phases; since the circular wall was presented during learning in all the conditions through this paper, we chose not to denote the cue in abbreviations of the conditions). During the learning phase, participants recalled the locations of four targets in the presence of both a circular wall and a cone array (Figure 2A). The cone array consisted of 18 traffic cones that were evenly distributed in a circle-like configuration. The wall was removed and the cone array was presented during the testing phase (Figure 2B). Based on the findings of Mou and Zhou (2013), we expected participants’ performance for remembering object location to be equivalent between the learning and testing phases in the ConeCirc-ConeCirc condition.

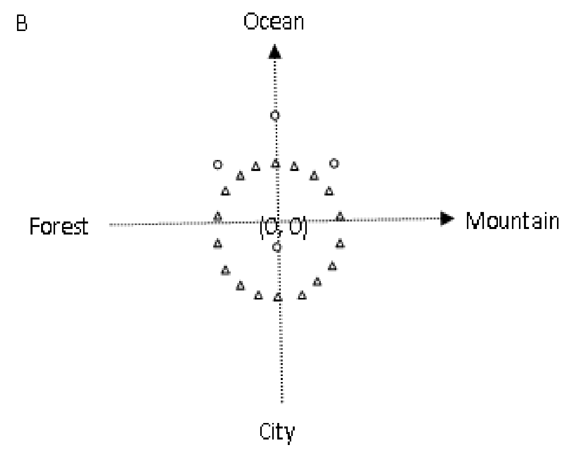
The cues presented during the learning phase were the same for the other three conditions (Figure 2C) while the global shape information from the testing cues was manipulated across those conditions. During the learning phase, a landmark array containing two arcs of traffic cones was presented together with the circular wall. Each arc of the cone array comprised nine cones, and the central angle of each arc was 90º (the angle subtended from the center to the two ends of the arc). This manipulation was to ensure that the landmark array provided the same number of reference points (thus the same number of individual vectors) as compared to the cone array (18) in the ConeCirc-ConeCirc condition.

The cues presented during the testing phase differed among the last three conditions. In the ConeArc-ConeArc condition (standing for the ‘two-arc cone array’ in addition to the wall used in the learning and the same cone array used in testing phases, see Figures 2C and 2D), the circular wall was removed and the two-arc cone array was presented during testing (Figure 2D). In the ConeArc-WallArc condition (standing for the two-arc cone array presented in addition to the wall during learning and the two wall arcs presented during testing), two arcs of the circular wall were presented alone during testing (Figure 2E). The central angle of each piece of the wall arcs (the angle subtended from the center to the two ends of the wall piece) was also 90º, and thus, comparable to the cone arc in the ConeArc-ConeArc condition during testing. In the ConeArc-ConeWallCirc condition (standing for the ‘two-arc cone array’ in addition to the wall used during learning and the ‘cone arcs and wall arcs forming a circular shape’ presented during testing), the two-arc cone array and the two arcs of the circular wall (the same as those used in the ConeArc-WallArc condition) were presented simultaneously during testing so as to form a circular configuration (Figure 2F). A contrast in the recall performance of object locations between the two conditions (ConeArc-ConeArc and ConeArc-WallArc) with a lack of global shape information at retrieval and the two conditions (ConeCirc-ConeCirc and ConeArc-ConeWallCirc) with the complete global shape at retrieval would support the shape-segment hypothesis.

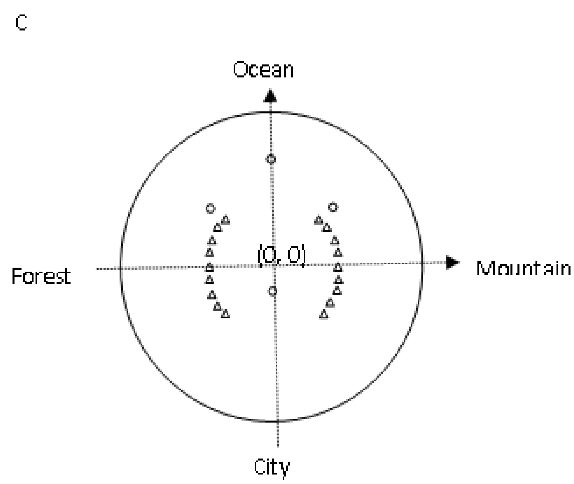
If multiple vectors are sufficient for encoding the target locations and the retrieval of the location memory, a comparable performance between the learning phase and the testing phase (i.e., null impairment effect from removing the wall during testing) would be expected in all four conditions as there were at least 18 reference points remained in the testing phase of all conditions. According to Mou and Zhou (2013), 18 reference points would be sufficient to eliminate the impairment effect. Alternatively, if the circular shape information obtained from the configuration of the test cues is important for participants to induce the original segmentation, an impairment effect from removing the surface boundary would be expected in ConeArc-ConeArc and ConeArc-WallArc.



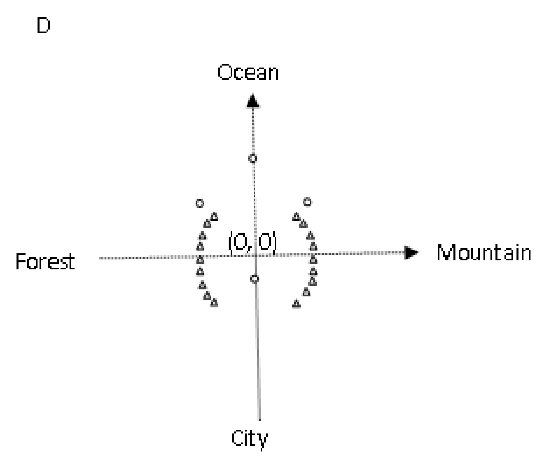
Learning of ConeCirc-ConeCirc



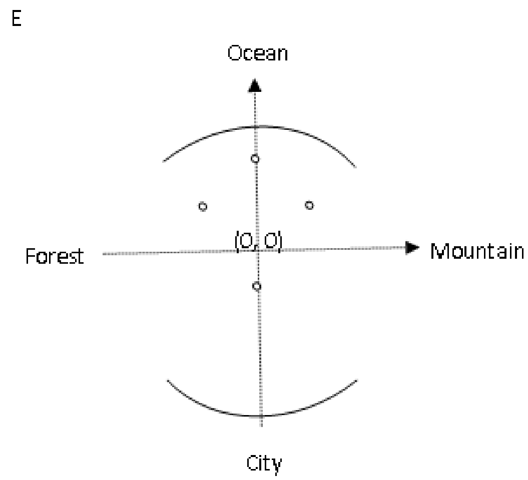
Testing of ConeCirc-ConeCirc



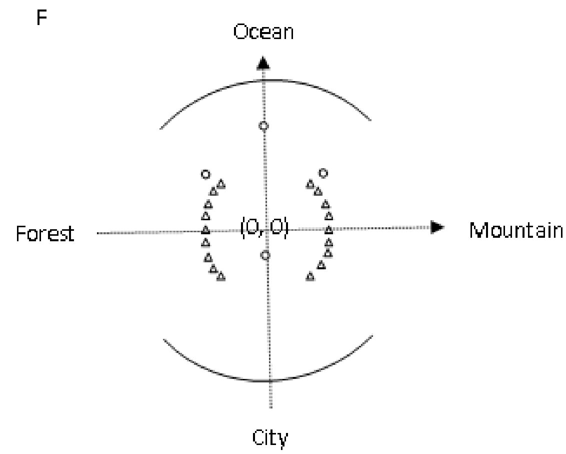
Learning of ConeArc-ConeArc, ConeArc-WallArc, ConeArc-ConeWallCirc



Testing of ConeArc-ConeArc



Testing of ConeArc-WallArc



Testing of ConeArc-ConeWallCirc

Figure 2. *Top-view illustrations of the experimental environments in Experiment 1. A illustrates the learning phase in the ConeCirc-ConeCirc condition. The outside circle depicts the circular wall. The four dots specify the target locations (only one target was visible at each learning/testing trial of the actual experiments); the small triangles mark the landmark array. Both the circular wall and the landmark array were centered at (0, 0) (the coordinates were not visible during the experiment). The axes depicting the coordinate system are to specify the spatial structure of the experimental environment for readers but were not shown during the experiment. The four labels, Ocean, City, Mountain, Forest, mark the orientation cues set at infinite distances. The orientation cues were presented as pictures corresponding to the labels in the actual experiment; B illustrates the cue configuration during the testing phase in the ConeCirc-ConeCirc condition; C, the environment of the learning phases in the ConeArc-ConeArc, ConeArc-WallArc and ConeArc-ConeWallCirc conditions; D, the cue configuration during the testing phase in the ConeArc-ConeArc condition; E, the cue configuration during the testing phase in the ConeArc-WallArc condition. The two arcs mark the two parts of the wall*

retained during testing; F represents the cue configuration during the testing phase in the ConeArc-ConeWallCirc condition.

Method

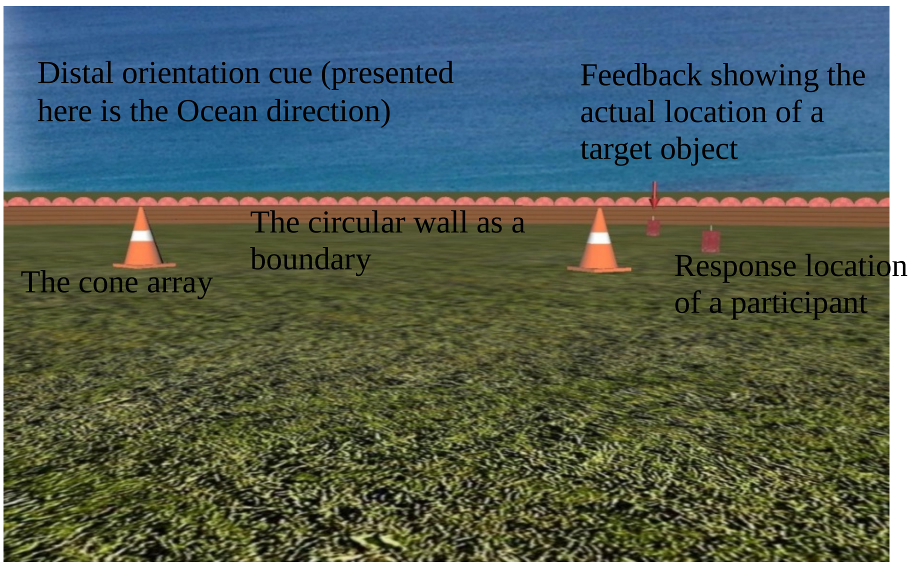
Participants

Seventy-two participants (36 men) were recruited for participation from introductory psychology courses at the University of Alberta. Participants received partial course credit for their participation.

Material and design

Participants learned four target locations in an immersive virtual reality environment. Orientation cues (Ocean, Forest, City and Mountain) were set at infinite distances on featureless grassland and were present throughout the entire experiment (see Figure 3 for snapshots of the virtual environment). The main task was to place four objects (wood, lock, candle and bottle) in their respective locations, (0, 38.18) [termed as Loc1], (19.09, 24.75) [termed as Loc2], (0, -5.66) [termed as Loc3], (-19.09, 24.75) [termed as Loc4] (units in virtual meters [vm], marked as the dots in Figure 2). The pairings between objects and locations were randomized across participants. Hence the locations are referred to according to their coordinates rather than their corresponding objects in our analysis sections (the four locations are labeled in Figure 2A). Participants completed four learning blocks (four trials per block, one trial per object within one block) in which feedback (object in its correct location) was given after each trial. Upon completing the learning phase, participants continued to the testing phase, which contained another four blocks of four trials without feedback. The sequence of objects within one block was randomized.

A



B

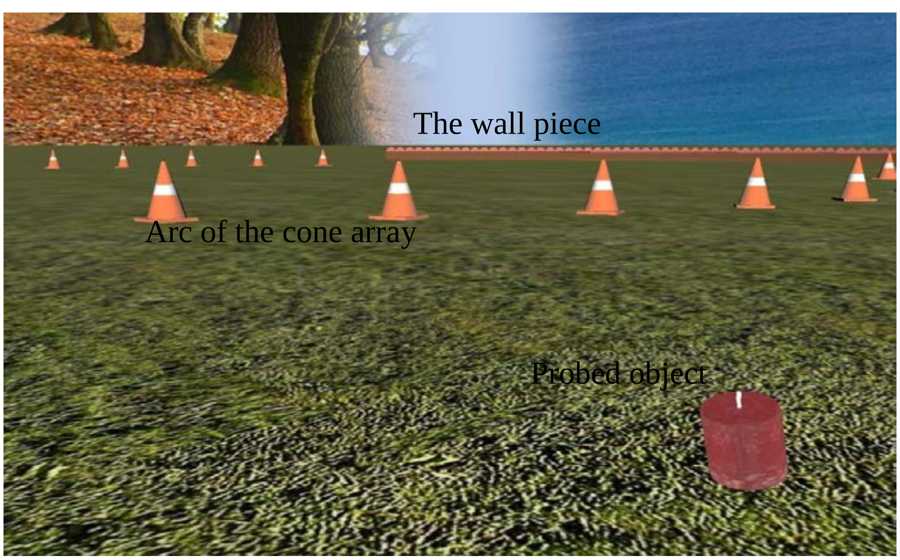


Figure 3. Snapshots of the virtual environment in Experiment 1 from a first-person perspective. A, the learning phase in the ConeCirc-ConeCirc condition; B, the testing phase in the ConeArc-ConeWallCirc condition.

Participants were randomly assigned to the four conditions consisting of different cue configurations. For the ConeArc-ConeArc condition, a circular wall (50 vm in radius, 1 vm in height) and a circular array of 18 traffic cones were presented as the cues during learning (Figure 2A). The two circles shared the same center (0, 0). Every two neighboring traffic cones in the cone array were 20 degrees in central angle (the cones are depicted as the triangles in Figure 2A) apart from each other (the array had a radius of 25.46 vm). Participants were then tested with the cone array alone (Figure 2B). Participants in the ConeArc-ConeArc condition were shown the circular wall and an 18-cone array in two arcs during learning. The circular wall was removed during testing, and the participants were shown the two-arc cone array alone. To create the two-arc cone array, we first made a circular array comprising the same 36 traffic cones (illustrated as the triangles in Figure 2C & 2D, two neighboring cones were 10 degrees in central angle apart from each other while the array had the radius of 25.46 vm). Only the nine cones corresponding to the direction of the Mountain and the nine cones corresponding to the direction of the Forest were used. The central angle for each arc was 90°. The participants in the ConeArc-WallArc condition learned the target locations in the same cue configuration as those in the ConeArc-ConeArc condition. However, the ConeArc-WallArc group was tested with two parts of the circular wall alone (Figure 2E). The retained two parts of the wall (depicted as the two arcs in Figure 2E) in this condition were created by segmenting the wall into four equal arcs corresponding to the four orientation cues and extracting only the arcs in the Ocean and the City directions. The central angle for each part of the wall was 90º. The learning phase in the

ConeArc-ConeWallCirc condition was the same as that of the ConeArc-ConeArc and the ConeArc-WallArc conditions (Figure 2C). The cue configuration during testing of the ConeArc-ConeWallCirc condition was a combination of the test conditions in the ConeArc-ConeArc and the ConeArc-WallArc conditions, i.e., both the two-arc cone array and the two parts of the wall were presented to form a circular configuration (Figure 2F). Eighteen participants were randomly assigned to one of the conditions with an equal number of men and women in each condition.

The experiment was conducted in a physical room of 4×4 m^2; however, participants never saw the physical room throughout the experiment. A swivel chair was placed at the center of the room (which corresponded to the center of the circular wall and the circular cone array). Participants were seated in the chair during the experiment and they could rotate the chair to change their orientations in the virtual reality environment.

The 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). Participants' head orientation was tracked with an InterSense IS-900 motion tracking system (InterSense, Inc., Massachusetts). Thus, through head rotation, participants could simply change their viewpoints. The height of the participants' viewpoint in the virtual environment was approximately 1.82 meters. Participants used a joystick to move forward and backward and to pick up and replace the objects in the environment.

The experiment used a mixed design with the experiment phase (learning vs. testing) as a within-subject factor and the cue configuration (ConeCirc-ConeCirc, ConeArc-ConeArc, ConeArc-WallArc and ConeArc-ConeWallCirc) as a between-subject factor. The distances between the correct locations and the response locations given by participants were defined as distance errors, which were used to measure participants' remembering of target locations given by specific environment cues. As in our previous paper (Mou & Zhou, 2013), we compared participants' performance between the learning and the testing phases to determine whether impairment effects were present. An impairment effect (greater distance errors during testing compared to the errors during learning) is expected if the remaining cue (the circular cone array, the two-arc cone array, the wall parts, or the combination of the wall parts and the cone array) was not sufficient for accurate recall of the target locations.

Procedure

After participants read the instructions, they were blindfolded and led to the experiment room. Participants sat in the chair and donned the HMD. They were first instructed to look around the virtual environment and to identify the orientation cues, the landmark array, and the circular wall by changing their head orientation. They were then trained to use the joystick to move forward and backward and to pick up and drop objects. To become familiarized with the virtual reality environment, participants were required to move to the edge of the wall in each of the four directions indicated by the orientation cues. Participants were then instructed to collect the four target objects as they successively appeared on the grassland of the environment. Each object was only collected once. This was to give participants a general idea about the to-be-learned targets and their locations.

Upon collection of all four targets, the learning phase started. Participants completed four blocks of four learning trials (one trial per target in each block). In each trial, one target appeared in the bottom right corner of the HMD screen, and participants attempted to place it in its original location. After their response, the same object was shown at its correct location to provide feedback regarding response accuracy. Participants then navigated to the correct location to pick up the object and continued to the next trial. The testing phase began after the 16 learning trials. Participants then finished four blocks of four testing trials (one trial per target in each block) with the pre-assigned testing cues. Feedback was not given during the testing phase. At the beginning of each trial throughout the experiment, including both the learning and the testing phase, participants were transported to start at a new random location (the starting locations were randomly picked within a circular area the radius of which is 50 vm), facing a random direction. This was to ensure that the target locations could not be specified by a fixed starting point or by the location of the target object probed in a previous trial.

Results

A data-exclusion criterion was determined prior to data analysis: any participant whose mean distance error during testing is greater than 100 vms would be excluded given that the radius of the wall was 50 vms. No participants were excluded in this experiment.

We measured distance errors (the distances between the correct locations and the response locations) as the dependent variable. There was a significant learning effect across the four learning blocks: distance errors (averaged across the four objects in each block) decreased in subsequent blocks, F (3, 204) = 22.08, $p < .001$, $\eta_p^2 = .25$. No practice effects were observed during the testing phase: the distance errors in remembering object locations remained flat across the four testing blocks, F (3, 204) = 2.07, $p = .105$, $\eta_p^2 = .03$. Hence, the distance errors in the last learning block indicated the acquisition of the location knowledge given by the corresponding learning cues, whereas distance errors averaged across the four testing blocks indicated the memory of the target locations relative to the corresponding testing cues. The learning effect across the four learning blocks and the lack of practice effect at test were also observed in Experiments 2. Therefore, in both experiments, we analyzed the distance errors in the last learning block and the distance errors averaged across the four testing blocks.

Figure 4 displays the mean distance errors as a function of cue configuration (the ConeCirc-ConeCirc, ConeArc-ConeArc, ConeArc-WallArc and ConeArc-ConeWallCirc conditions) and the experimental phase (the last learning block vs. all testing blocks). As shown in Figure 4, there was a significant increase in the magnitude of the distance errors during the entire testing phase compared to the last learning block in the ConeArc-ConeArc and the ConeArc-WallArc conditions; this increase indicates an impairment effect in both groups upon the removal of the partial cues. However, there was no impairment effect observed in either the ConeCirc-ConeCirc or the ConeArc-ConeWallCirc conditions. Further analysis with mixed-model ANOVAs confirmed this observation, with cue configuration (ConeCirc-ConeCirc, ConeArc-ConeArc, ConeArc-WallArc and ConeArc-ConeWallCirc) as a between-subject variable, and the experimental phase as a within-subject variable.

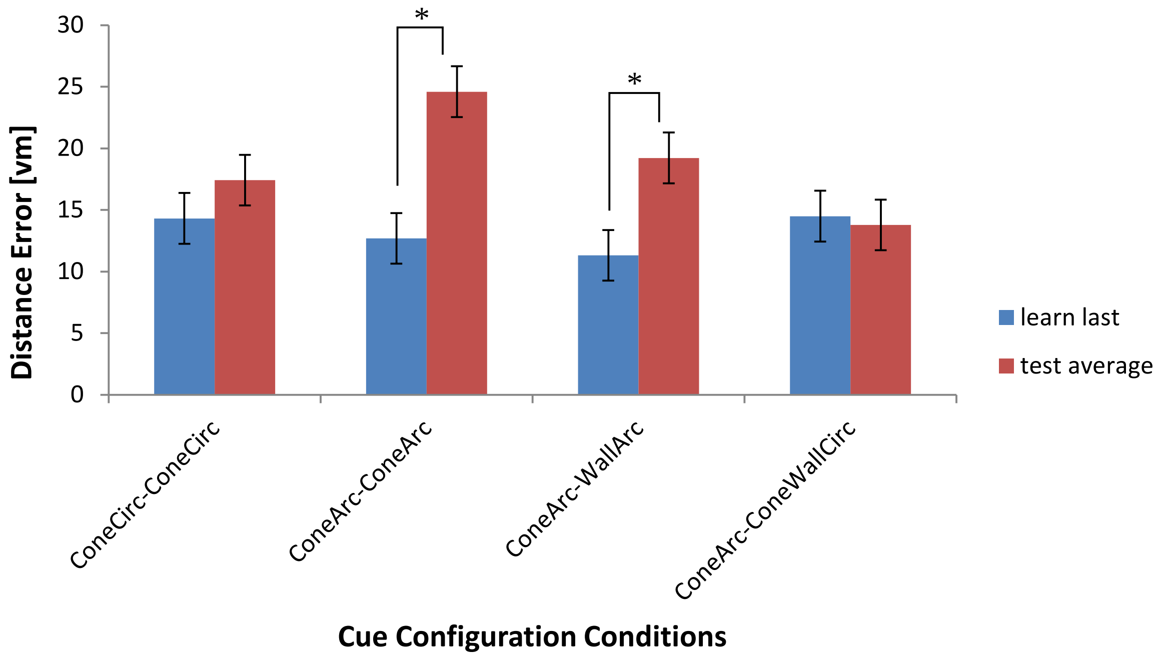


Figure 4. Distance errors as a function of cue configuration and experimental phase in Experiment 1 (Error bars are ± 1 standard error after removing the between-subject variation).

The main effect of the experimental phase was significant: F (1, 68) = 14.54, $p < .001$, η_p^2 = .18. The main effect of the cue configuration was not evident: F (3, 68) = .59, p = .62, η_p^2 = .03. The interaction between the cue configuration and the experimental phase was significant: F (3, 68) = 3.59, p = .02, η_p^2 = .14.

Planned comparisons (using a two-tailed t-test) revealed greater distance errors during the testing phase than during the learning phase in both the ConeArc-ConeArc condition, t (68) = 4.09, $p < .001$, and the ConeArc-WallArc condition, t (68) = 2.72, p = .008. However, distance errors did not increase in magnitude in either the ConeCirc-ConeCirc condition, t (68)

= 1.07, p = .29, or the ConeArc-ConeWallCirc condition, t (68) = .25, p = .81. A one-way ANOVA on the distance error at the last learning block confirmed that there is no difference in participants' performance towards the end of learning phase across the four cue configuration conditions, F (3, 68) = .52, p = .67, η_p^2 = .02. The lack of difference in learning performance indicated that the impairment observed in the two conditions where the global circular shape was disrupted was not due to do any insufficient learning.

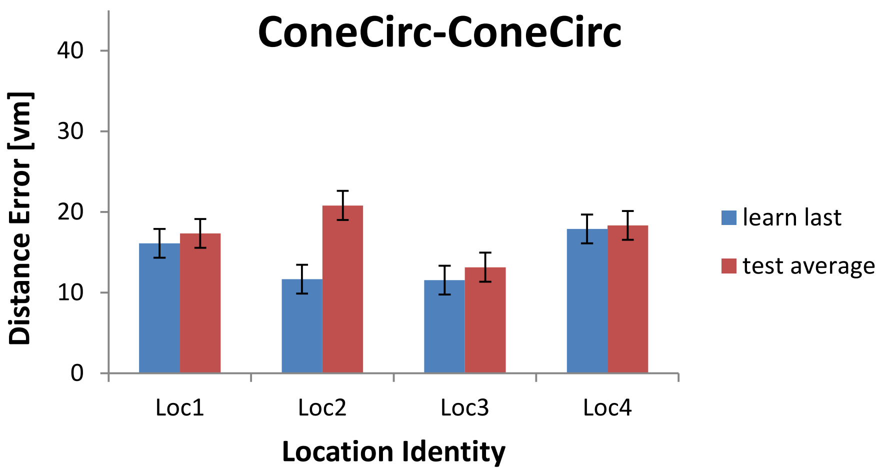
According to the shape-segment hypothesis, segments closer to the target locations could be selected as the reference points for encoding individual locations, we expect that removing different parts of the cone array or the wall might have differential effect on memory performance for different target locations. That is, for instance, removing the wall parts facing the ocean direction might exert more impairment on location memory for Loc1 (Figure 2A&D). Therefore, in addition to the experimental phase and the cue configuration, we also include the location identity (i.e., Loc1-4) as a within-subject variable in a three-way factorial analysis to further examine whether location memory differed for different target locations depending on the cue configuration during testing.[1]

Our analysis revealed a significant 3-way interaction among the experiment phase, the location identity and the testing cue configuration, F (9, 204) = 2.05, p = .036, η_p^2 = .08. We conducted four separate two-way ANOVAs examining the interaction of the experiment phase and the location identity in all testing cue conditions. Interaction of the experiment phase and the location identity was not significant in any of the four conditions, ConeCirc-ConeCirc, F (3, 51) = 2.55, p = .07, η_p^2 = .13, ConeArc-ConeArc, F (3, 51) = 1.90, p = .14, η_p^2 = .10, ConeArc-WallArc, F (3, 51) = 1.80, p = .16, η_p^2 = .10, and ConeArc-ConeWallCirc, F (3, 51) = 1.65, p = .19, η_p^2 = .09. Memory decrease during testing was observed for all four locations in ConeArc-

[1]We thank the two anonymous reviewers for suggesting further analysis to examine the differential effect of cue configuration during testing on different target locations.

ConeArc, F (1, 17) = 5.20, p = .04, ŋp2 = .23 and in ConeArc-WallArc, F (1, 17) = 22.25, p < .001, ŋp2 = .57. In contrast, no decrease in object location memory was observed in ConeCirc-ConeCirc, F (1, 17) = 3.82, p = .07, ŋp2 = .18, or in ConeCirc-ConeWallCirc, F (1, 17) = 0.40, p = .54, ŋp2 = .02, where the global shape segmentation was intact during testing.

A



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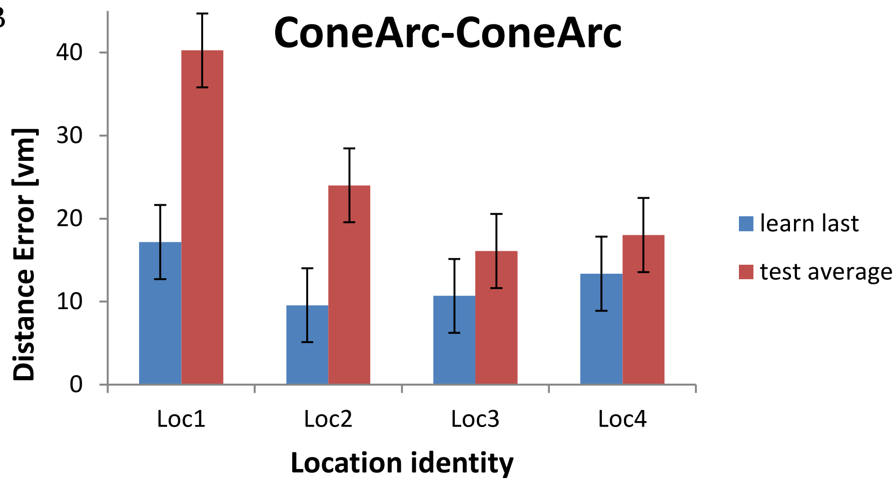

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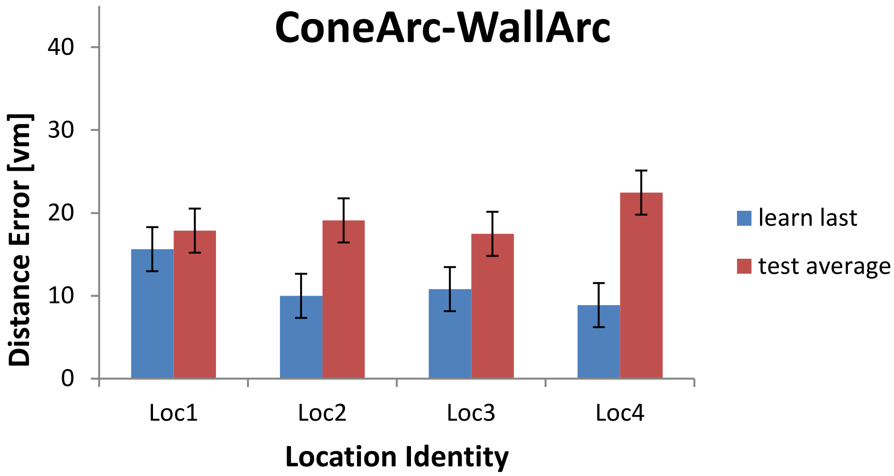
ConeArc-WallArc
Distance Error [vm]
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10
20
30
40
Loc1
Loc2
Loc3
Loc4
Location Identity
learn last
test average

D

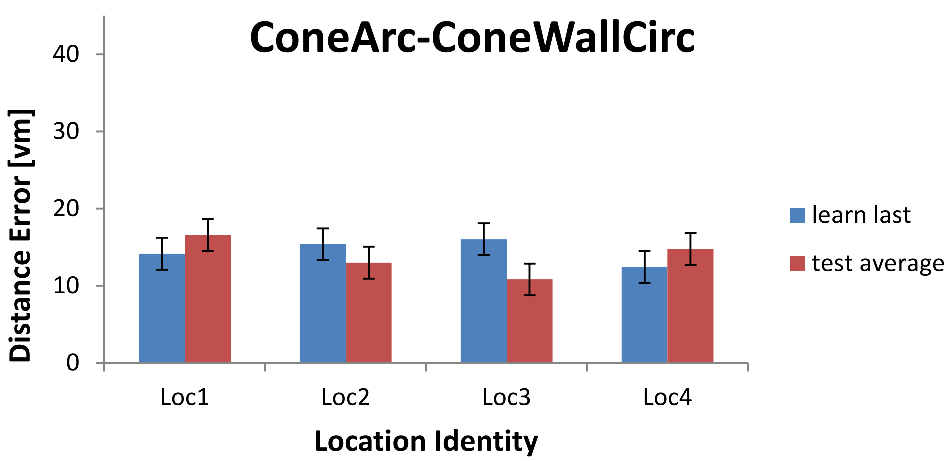

ConeArc-ConeWallCirc
Distance Error [vm]
0
10
20
30
40
Loc1
Loc2
Loc3
Loc4
Location Identity
learn last
test average

Figure 5. Distance errors as a function of location identity and experimental phase across four conditions of cue configurations in Experiment 1 (Error bars are ± 1 standard error after removing the between-subject variation). A, the ConeCirc-ConeCirc condition; B, the ConeArc-ConeArc condition; C, the ConeArc-WallArc condition; D, the ConeArc-ConeWallCirc condition.

Discussion

The results of Experiment 1 support the shape-segment hypothesis rather than the sufficient-reference-points hypothesis. According to the shape-segment hypothesis, the global shape of the circular wall affected the selection of reference points for encoding target locations. In particular, this global circular shape together with the distal orientation cues enables participants to differentiate the segments of the wall. Participants further encode a given location with respect to the differentiated segments. A disruption of the global shape integrity during testing would likely impede the recovery of the original segmentation acquired from learning, as we can see from the impaired performance in the ConeArc-ConeArc and ConeArc-WallArc conditions. By contrast, participants in the ConeArc-ConeWallCirc and the ConeCirc-ConeCirc conditions were able to recover the original circular shape (for instance, by integrating the wall parts and the cone arcs in the ConeArc-ConeWallCirc condition), demonstrating intact location memory during testing. These findings challenged the sufficient-reference-points hypothesis, which stipulates that only the number of the reference points during testing is critical in accurate recall of target locations. According to this hypothesis, null impairment effect would be observed in any conditions as the number of reference points during testing was sufficient (i.e. 18 or more); our results however were inconsistent with this prediction.

Further analysis on the differential effects of cue configuration on memory performance for different target locations revealed no interaction effect between the experiment phase and the location identity in any of the four cue-configuration conditions. This result again demonstrates that the global shape formed during testing is critical for recalling the target locations: a disruption in recovering the segmentation during testing interferes object location memory.

In addition to providing reference points for encoding locations, a boundary also provides scale information for objects residing within the enclosure. One possible explanation for the decreased performance during testing of ConeArc-ConeArc and ConeArc-WallArc is that the absence of a complete wall also eliminated this scale information. Note that in the ConeCirc-ConeCirc condition, three of the four targets were outside the circular cone array. Participants were able to retain their object-location memory without the outmost boundary, suggesting that they were able to encode the distance information from the inner cone circle.

Experiment 2

Experiment 2 is designed to provide further evidence for the shape-segment hypothesis. Participants learned four target locations relative to two eccentric circles, one formed by a continuous wall and the other formed by a cone array. They were subsequently tested (by replacing the objects to their original locations) when either circle was removed. The question is whether an impairment effect (decreased object location memory during testing) would be observed due to the removal of one circle. The number of the cones was 36 (a 36-cone array), which should be sufficient to eliminate the impairment effect upon the removal of the wall. This lack of impairment effect was demonstrated in Mou and Zhou's study (2013) as well as in the Experiment 1 of the current study, where the cone array (containing 18 or more cones) was concentric with the wall. The shape-segment hypothesis predicts an impairment effect upon the removal of either circle because the two eccentric circles would produce two independent segmentations (e.g., Figure 1B) and participants might not be able to simultaneously utilize both. In contrast, the sufficient-reference-points hypothesis predicts no impairment effect upon the removal of either circle because the number of the reference points during testing should be sufficient.

Method

Participants

Forty-nine undergraduate students (24 men) were recruited for participation from an introductory psychology course of the University of Alberta. One female participant was excluded from the sample because her mean distance error across the four test blocks was greater than 100 meters. All participants received partial credit for their participation.

Material, design and procedure

The center of the 36-cone array (the cones were evenly spaced and are depicted as the triangles in Figures 6A and 6C) was located at the coordinates (0, -16.26) (illustrated as the square in Figures 6A and 6C) so that the wall and the cone array were eccentric. The participants were randomly assigned to two groups with 24 participants (12 men) in each group. Both groups learned the target locations with two cues presented (both the circular wall and the circular cone array). The boundary group (referred to as LB-B) was tested with only the circular wall (Figure 6B), whereas the landmark group (referred to as LB-L) was tested with only the cone array

(Figure 6C). The orientation cues were presented during the entire experiment. The rest of the design and the procedure were identical to those in Experiment 1.

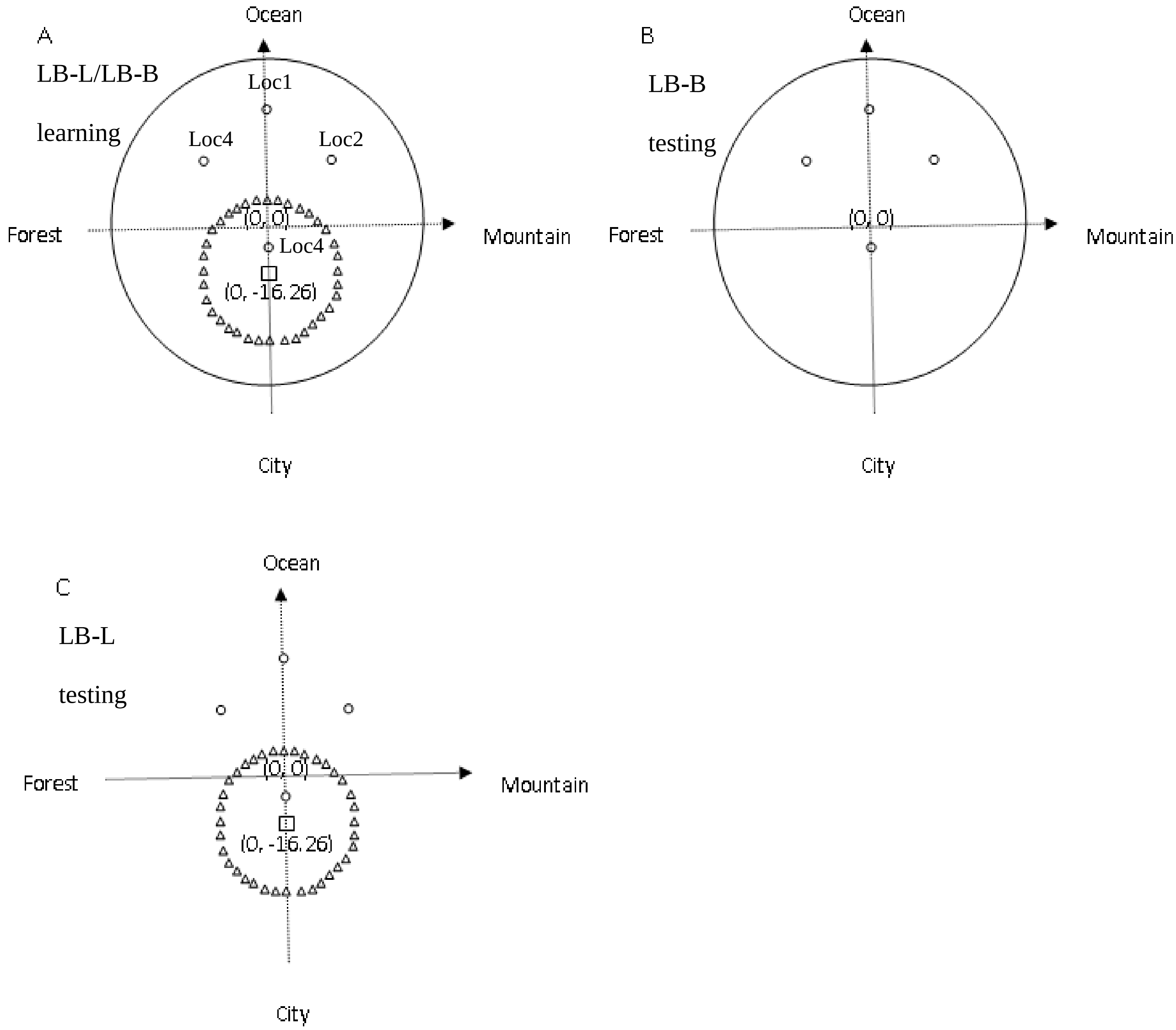


Figure 6. *Top-view illustrations of the experimental environment in Experiment 2. A illustrates the learning environment in both the LB-L and the LB-B conditions. The square marks the center of the cone array, which was not displayed during the actual experiment. B illustrates testing environment in the LB-B condition. C illustrates the testing environment in the LB-L condition.*

Results and discussion

Figure 7 displays the mean distance errors plotted as a function of the experimental phase (the last learning block vs. the average of the four testing blocks) and the testing cue (LB-B vs. LB-L). As shown in Figure 7, the impairment effect was observed in both conditions. Repeated-measure ANOVAs using the testing cue as a between-subject variable and experimental phase as a within-subject variable confirmed this observation.

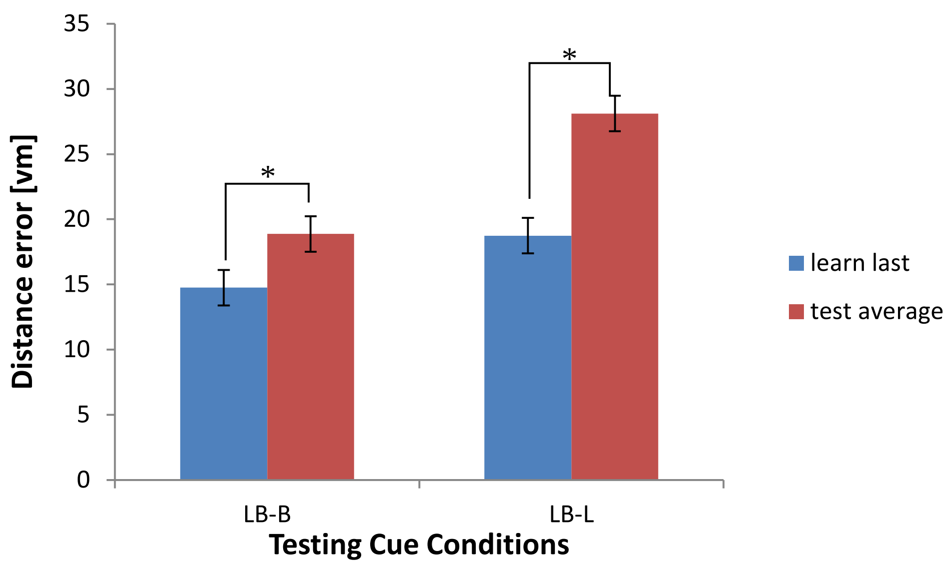


Figure 7. Distance errors as a function of the testing cue and experimental phase in Experiment 2 (Error bars are ± 1 standard error after removing the between-subject variation). LB-B: learning with both the wall and the shifted cone array while testing with the wall; LB-L: learning with both the wall the shifted cone array while testing with the cone array.

The main effect of experimental phase was significant: F (1, 46) = 24.56, p < .001, η_p^2 = .35. The main effect of testing cue was also significant: F (1, 46) = 9.05, p = .004, η_p^2 = .16. The interaction between these two variables was not significant: F (1, 46) = 3.72, p = .06, η_p^2 = .08. Planned comparisons (two-tailed t-tests) revealed greater distance errors during testing than during the fourth learning block in both LB-B, t (46) = 2.14, p = .04, and LB-L, t (46) = 4.87, p < .001.

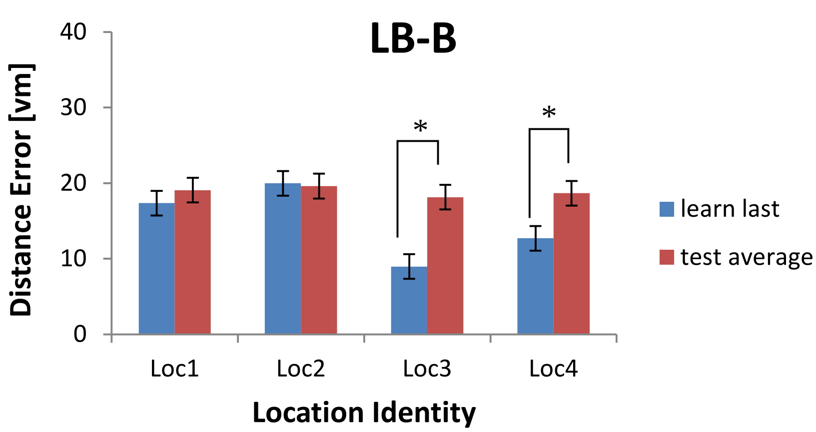
These results indicated that the removal of either the circular wall or the cone array impaired memory retrieval of target locations, which was consistent with the prediction based on the shape-segment hypothesis but not on the sufficient-reference-points hypothesis.

Although the interaction effect was not significant (F (1, 46) = 3.72, p = .06, η_p^2 = .08), Figure 7 showed that the larger distance error in the LB-L than in the LB-B might primarily occur during testing. Note that LB-L and LB-B are identical in the learning phase so we should not expect any difference in distance errors in the testing phase. A two-sample t-test was carried out to examine the distance errors (averaged across the four probed locations) between the two conditions. Participants displayed equivalent learning performance for location memory in the two conditions, t (46) = -1.79, p = .08. Thus, the main effect of testing cue (whether the cone array or the wall alone was presented during testing) was mainly driven by the more pronounced decrease in location memory in LB-L than in the LB-B. One explanation could be that when participants used both wall and the *shifted* cone array to encode object locations independently, these two cues competed. The shifted cone array might be a less effective cue than the wall because (a) the cone array was smaller than the wall and (b) the shifted cone array overall was further away from the target locations than the wall if we assume people prefer a more stable and also closer cue. Hence, there was a larger impairment effect by removing the wall than by removing the cone array. Note that participants in Experiment 1 (ConeArc-ConeArc) used both wall and the *concentric* cone array to encode object locations dependently. Hence, removal of either cue did not affect remembering the target locations.

We conducted further analysis to examine whether the testing cues exerted differential effects on location memory performance for different probed locations. A three-way ANOVA was conducted with the testing cue as the between-subject variable, the experimental phase and the location identity (i.e., Loc1-4) as the within-subject variables. A three-way interaction was revealed, F (3, 138) = 3.20, p = .025, η_p^2 = .065. Two separate two-way ANOVAs examined the interaction of the experimental phase and the location identity for LB-L and LB-B conditions, respectively. Interaction was significant only for LB-B, F (3, 69) = 3.44, p = .02, η_p^2 = .13, but not for LB-L, F (3, 69) = 1.50, p = .22, η_p^2 = .06. Specifically, paired-sample t-test revealed a decrease in memory performance for Loc3, t (23) = 3.98, p < .001, and for Loc4, t (23) = 3.28, p = .002 whereas memory performance was retained for Loc1, t (23) = 0.74, p = .23 and Loc2, t (23) = 0.16, p = .44. This result indicates that reference points available in the environment are not treated equally. The shape segment process enables participants to differentiate the available reference points (wall parts or cones closer to the Ocean direction in Fig. 6A) and they subsequently chose relevant reference points for encoding a specific target (e.g., the wall part closer to Loc1). Removing these more informative reference points would impair the corresponding location memory (e.g., decreased memory for Loc3 and retained memory for Loc1 when only the wall was presented in LB-B). In contrast, the sufficient-reference-points hypothesis would imply that all reference points are treated equal.

Note that in the current project, we only contrast the shape-segment hypothesis and the sufficient-reference-points hypothesis. A distance-based hypothesis claiming that participants only selected reference points based on the distances to individual targets could also explain the current data. For example, the object in the center (Loc3) is closer to the cone array (shorted distance = 14.86 vm) than to the boundary (shortest distance = 44.34) so people use the cones to encode this object. We acknowledge that this hypothesis can explain the current data (e.g. the impairment effect for Loc3 in LB-B). However, this hypothesis was inconsistent with the finding of Mou and Zhou (2013). In their Experiment 2, participants learned the same four locations relative to a cone array and a wall as in *ConeCirc-ConeCirc*. The distance-based hypothesis should predict that removal of the cone array in the test phase would produce an impairment effect because at least three locations were encoded relative to the cone. However, Experiment 2 of Mou and Zhou (2003) did not find any impairment effect due to the removal of the cones. In addition, a smaller impairment effect was also observed for Loc 4 in LB-L whereas memory for all four locations were impaired in ConeArc-ConeArc and in ConeArc-WallArc regardless of the distance between the probed locations and removed wall/array parts. Therefore, such distance-based hypothesis was inconsistent with the finding of Experiment 1.

A



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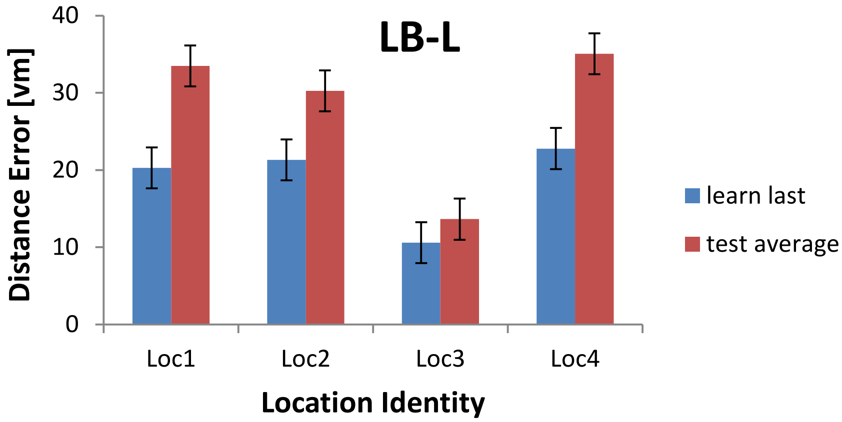

Figure 8. Distance errors as a function of location identity and experimental phase between the two testing-cue conditions in Experiment 2 (Error bars are ± 1 standard error after removing the between-subject variation). A, LB-B; B, LB-L.

General Discussion

This study investigates the role of the global shape of a boundary in encoding and remembering locations of target objects. In particular, we distinguish between the shape-segment hypothesis and the sufficient-reference-points hypothesis derived from the vector-based localization models (Cheng, 1989; O'Keefe & Burgess, 1996; Mou & Zhou, 2013). The shape-segment hypothesis acknowledges the importance of the global shape formed by multiple reference points in localization. However, the sufficient-reference-points hypothesis emphasizes the importance of the number of individual reference points in localization but overlooks the importance of the global configuration formed by the reference points. Our findings favor the shape-segment hypothesis over the sufficient-reference-points hypothesis.

The sufficient-reference-points hypothesis derived from the vector-based models, including the BVC model (O'Keefe & Burgess, 1996), the multiple-reference-point hypothesis

(Mou & Zhou, 2013) and the vector-sum model (Cheng, 1989), focuses on the importance of individual vectors established between a target location and a number of reference points provided by an environmental cue. A larger number of reference points providing more individual vectors contribute to a more accurate representation of a target location until there are a sufficient number of reference points (i.e., 18 or more cones, Mou & Zhou, 2013). Therefore, accuracy in remembering of target locations does not decrease when removing some reference points as long as the total number is sufficient during testing. By contrast, according to the shape-segment hypothesis, apart from individual vectors, presenting a larger number of discrete reference points also leads to a higher likelihood that people perceive the shape formed by these reference points. When people perceive such shape information, they segment the shape into local parts, differentiate those parts using orientation cues, and then encode a given target location relative to the differentiated segments. A similar shape-segment process occurs during testing to re-identify the original reference points used in the learning phase. Therefore, object location memory decreases upon the removal of some reference points that impairs the recovery of the original segmentation.

Experiment 1 showed that the global shape formed by the testing cues was critical in eliminating the impairment effect resulted from removing the wall or parts of the wall that was presented during learning, favoring the shape-segment hypothesis. Four groups of participants (ConeCirc-Cone-Circ, ConeArc-ConeArc, ConeArc-WallArc and ConeArc-ConeWallCirc, Figure 2) learned four locations relative to both the cone array and the circular wall. Although there were equal amounts of cones (18) available during learning in all the four conditions, the cone array in the ConeCirc-ConeCirc group formed a circle while the arrays in the other three conditions did not. Participants were tested subsequently with the landmark array alone (in the

ConeCirc-ConeCirc and ConeArc-ConeArc conditions), two parts of the wall maintaining the same visual angle as the two parts of the non-circle array (the ConeArc-WallArc condition) or the combination of the wall parts and the array together forming a circular shape (the ConeArc-ConeWallCirc condition). The poorer object location memory in the testing phase compared to that in the learning phase (i.e. the impairment effect due to the removal of the corresponding environmental cues) was observed when the configurations of the testing cues were not consistent with the original shape of the wall (i.e. a circular shape), but the spared recall performance was observed when the global configurations of the testing cues echoed with the original shape of the wall.

This finding was consistent with the shape-segment hypothesis. According to the shape-segment hypothesis, the disruption of the global shape during testing of ConeArc-ConeArc and ConeArc-WallArc (the circular configuration was provided by the wall during learning) would likely disrupt the recovery of the original segmentation, causing the impairment effect in retrieving the location memory. In contrast, our findings challenged the sufficient-reference-points hypothesis. It is hard for this hypothesis to explain why the global shape during testing should matter (e.g., the contrast between ConeArc-ConeWallCirc and ConeArc-coneArc/ConeArc-WallArc). Furthermore, the sufficient-reference-points hypothesis also has difficulty in explaining why there was impairment effect in the ConeArc-ConeArc condition but not in the ConeCirc-ConeCirc condition (Figure 2). According to the sufficient-reference-points hypothesis, because there were equal amounts of reference points during testing in the ConeArc-ConeArc and the ConeCirc-ConeCirc conditions, there should be no impairment effect in the ConeArc-ConeWallCirc condition as there was no impairment effect in the ConeCirc-ConeCirc condition.

Experiment 2 showed the impairment effect in object location memory due to the removal of either the circular wall or the cone array during testing, when the wall and the circle formed by the cone array were eccentric during learning. This finding was again consistent with the prediction of shape-segment hypothesis. According to the shape-segment hypothesis, two concentric circles create two completely aligned segmentations (Figure 1A). Furthermore, the corresponding segments (aligned in allocentric directions) in the two circles have a fixed distance in between (i.e. the radius difference) across all directions. Therefore, the vector from a target to the segment of one of the circles can be used to infer the vector to the corresponding segment of the other circle, and vice versa. Hence, the removal of either circle during testing should not affect location memory. Conversely, two eccentric circles create two independent segmentations (Figure 1B). A competition could occur between the two segmentations; hence, an inability to use both cues is expected. Consistent with this prediction, the impairment effect was observed when either circle was removed during testing. Our finding however was inconsistent with the prediction from the sufficient-reference-points hypothesis. According to the sufficient-reference-points hypothesis, as long as there is enough number of reference points during testing, irrespective of whether the circle formed by the landmark array was concentric or eccentric with the wall, removing the wall should not impair performance in recall of learned object locations. The number of the reference points during testing in Experiment 2 should be adequate for recovering the location memory as suggested in Experiment 1 of the current study (ConeCirc-ConeCirc condition) as well as in Mou and Zhou (2013). Therefore, the sufficient-reference-points hypothesis would not predict any impairment effect for Experiment 2.

In Experiment 2, we observe that the testing cues/configuration elicited differential impairment effect on the probed locations depending on the distance between the removed parts and the target locations (Loc3 and Loc4 in LB-B). The shape-segment hypothesis could explain the differential effect. The global shape/configuration provides a way for participants to segment the reference points. For example, a circular shape can be divided into 12 directions (like the clockface) and 12 reference points could be segmented from the circular enclosure. Then each target will be encoded with respect to the closest reference point rather than to all the 12 reference points. In contrast, the sufficient-reference-points hypothesis implies that all reference points are treated equally and each might be used for encoding the target location. Therefore, according to the **shape-segment** hypothesis, removing reference points in specific directions during testing would impair location memory for the locations encoded relative to the removed reference points. Different impairment effect would be observed for different target locations.

The shape-segment hypothesis, as opposed to the sufficient-reference-points hypothesis, underscores one important difference between a boundary cue and a single landmark cue in goal localization. According to sufficient-reference-points hypothesis (see also the multiple reference point hypothesis proposed by Mou & Zhou, 2013), a surface-based boundary or a landmark array forming a certain geometric shape could provide multiple vectors in encoding a target location, whereas a single object-based landmark can only provide a single vector. Thus, the difference between a boundary and a landmark might be quantitative: single vs. multiple vectors. According to the shape-segment hypothesis, the difference might also be qualitative, where the global shape knowledge extracted from the configuration of multiple reference points could be regarded as distinctive from the elemental knowledge of a single vector.

By emphasizing the importance of global shape information in a location memory task, the shape-segment hypothesis also links the goal localization literature to the reorientation literature, which has already established the importance of global shape information in reorientation. The difference between reorientation tasks and object-location memory tasks might not be as significant as it appears (e.g. Burgess, 2008; Lew, 2011). From the perspective of the shape-segment hypothesis, the first stage during the encoding of a target location (i.e. segmenting a shape to parts and differentiate the parts by orientation cues) might also be applied in a reorientation task (Miller & Shettleworth, 2007). In a typical reorientation task, participants learn a target placed at one corner of a rectangular room that also contains some unique features to distinguish the correct corner from its diagonal counterpart. After disorientation, participants search for the target (e.g. Cheng, 1986). According to the shape-segment hypothesis, when participants learn a target location, they might possibly segment the room into four corners and four walls. They then use the geometry information (e.g. the principal axis, Gallistal, 1990) to distinguish between two geometrically different pairs of corners, the pair on the left side of the body vs. the pair on the right side of the body, when the body is aligned with the principal axis of the room. Therefore, during testing, people can still distinguish between these two pairs of corners relying on the geometry information of the room and search at the correct corner and the diagonal (geometrically identical) corner. Such use of abstract geometric information (including distance and sense of direction) seems to developed at an early age as 2-year-old children are already able to reorient themselves based on the distance and direction information extracted from room geometry (e.g., Lee, Sovrano & Spelke, 2012).

The reorientation tasks and the tasks probing object location memory might also share the similar cognitive mechanisms when participants are selecting between a continuous boundary and a single landmark as their primary spatial cue. The adaptive-combination theory was proposed to explain why participants ignored the featural cues that in principle would help them avoid the diagonal corner in reorientation tasks (Newcombe & Ratliff, 2007; Ratliff &

Newcombe, 2008). This theory speculates that although both a landmark and the shape based on a boundary can be used to reorient, the cue selected depends on the relative salience of the cues; since in general a shape is more salient than a landmark, people are more likely to ignore the featural cues. The neural underpinnings of such reliance on global geometry to regain one's sense of direction have also been identified in a recent electrophysiological study (Keinath, Julian, Epstein & Muzzio, 2017). In accordance with the adaptive-combination theory and the empirical evidence, the shape-segment hypothesis also speculates that both a shape and a landmark can be primarily used in goal localization. The cue selection process depends on the relative salience of the cues and thus, people tend to use the shape based on a boundary but ignore the landmark as a reference cue for encoding a target location. This hypothesis can explain why the impairment effect resulted from removing a continuous boundary occurred after participants learned the target locations with compound cues (a boundary and a single landmark) in the previous studies (Doeller & Burgess, 2008; Mou & Zhou, 2013) and in Experiment 1 (the *ConeArc-ConeArc* condition) of the current study.

One thing to be noted here is that the environmental cues in the current study were mostly organized in a circular shape (also in our previous study, Mou & Zhou, 2013). This design, to a certain degree, would limit the generalization of the shape-segment hypothesis when applied to cases where the environmental cues would form irregular shapes. To determine how people possibly segment an environment when the global shape becomes hard to perceive would demand a similar paradigm using a continuous boundary and a landmark array forming some irregular shapes. Future studies should be conducted to address such issue.

In summary, this study showed that the global shape formed by the testing cues was important for encoding locations: when the global shape information obtained at retrieval was consistent with the global shape (i.e. a circle) formed by the learning cues, recall of object locations was not impaired; otherwise, location memory was impaired. These findings support the proposal that while individual reference points provided by a boundary are important for establishing vectors between the local references and targets, the global shape of a boundary affects the segmentation process and the subsequent selection of local reference points for encoding locations.

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Open Practices Statements

None of the data or materials for the experiments reported here is available, and none of the experiments was preregistered.

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