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Two-category place representations persist over body rotations

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Abstract We explored a system that constructs environment-centered frames of reference and coordinates memory for the azimuth of an object in an enclosed space. For one group, we provided two *environmental cues* (doors): one in the front, and one in the rear. For a second group, we provided two *object cues*: a front and a rear cue. For a third group, we provided no external cues; we assumed that for this group, their reference frames would be determined by the orthogonal geometry of the floor-and-wall junction that divides a space in half or into multiple territories along the horizontal continuum. Using Huttenlocher, Hedges, and Duncan's (*Psychological Review* 98: 352–376, 1991) category-adjustment model (cue-based fuzzy boundary version) to fit the data, we observed different reference frames than have been seen in prior studies involving two-dimensional domains. The geometry of the environment affected all three conditions and biased the remembered object locations within a two-category (left vs. right) environmental frame. The influence of the environmental geometry remained observable even after the participants' heading within the environment changed due to a body rotation, attenuating the effect of the front but not of the rear cue. The door and object cues both appeared to define boundaries of spatial categories when they were used for reorientation. This supports the idea that both types of cues can assist in environment-centered memory formation.

Keywords Place memory · Coarse-grain representation · Environmental geometry · Landmark · Category · Bias

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When people encode where they are placing an object (e.g., a key), they encode the direction and distance of the object relative both to themselves (egocentric coding; Wang et al., 2006; Wang & Spelke, 2000, 2002) and to nearby objects and other features of the environment (allocentric coding; Gallistel, 1990; O'Keefe & Burgess, 1996). The environmental features used for allocentric coding can be subcategorized into environmental landmarks and object landmarks. *Environmental landmarks* include architectural structures such as corners, doorways, and the boundaries or geometric shape of the environment. *Object landmarks* refer to salient nontarget objects (e.g., a color patch, a floor lamp) situated among the environmental landmarks. Environmental landmarks play a role in constructing environment-centered frames of reference, define possible paths for navigation, and specify reference directions that can be used for reorientation (Carr & Watson, 1908). In addition, environmental landmarks are thought to be more stable cues than object landmarks (Lew, 2011). Location stability can be conceptualized as being proportional to the geometric salience of a given location or to the inverse variance of the location representation. Environmental landmarks indicate the most stable framing locations, whereas the stability of object landmarks declines as their distance from a stable framing element increases. Evidence from the animal literature has indicated that environmental and object landmarks have distinct roles in orientation processes and engage different neural substrates (see Lew, 2011, for a review); in this literature, however, the *stability* of the landmark locations is thought to be a more crucial factor than *landmark type* for determining which brain structures are recruited. The striatum has been reported to support the learning of unstable cue-based localization, whereas the hippocampus is thought to mediate the learning of stable cue–environment associations, and thus to mediate place recognition more generally (e.g., McDonald & White, 1994). The extent to which these types of landmarks might be processed differently in human visual and memory systems remains unclear. We investigate this issue in the present article.

Frames of reference play a crucial role for encoding and remembering object locations, because the location coordinates must be specified relative to some reference frame. Importantly, location judgments can become biased relative to salient reference frame axes. Huttenlocher, Hedges, and Duncan (1991) introduced a category-adjustment model and explained localization bias in terms of two levels of spatial encoding. On the fine-grain level, the target location is encoded in terms of a coordinate system composed of virtually continuous dimensions. On the coarse-grain level, the target location is encoded in terms of a coordinate system composed of categories that divide the domain of interest into geometrically distinct sectors. In domains in which environmental geometry is less salient than the distribution of object locations, Huttenlocher et al. predicted different spatial categories corresponding to distinct clusters of objects. The center of each category can serve as a *prototype*, whereas the border of two neighboring categories can serve as a *boundary*. The category-adjustment model predicts inward bias within the borders of each category: that is, location misestimates away from the boundary and toward the prototype. Note that in addition to layout geometry (sectors) and object distributions, external cues can also be used to define spatial categories (e.g., dot cues functioned as prototypes in Fitting, Wedell, & Allen, 2005, 2007). The category-adjustment model, however, only accounts for prototype-driven categories, and does not account for situations in which cues define spatial categories as boundaries. In order to predict when cues will function as boundaries versus prototypes, we further factored in the stability of the cue locations and introduced two category-association assumptions. First, environmental landmarks can divide geometric categories, and thus serve as boundaries (and object location estimates will then be biased *away* from these boundaries), whereas means of object distributions serve as prototypes (and thus, location estimates will be biased *toward* these means). Second, when object landmarks are visible close to environmental landmarks (e.g., near the wall of an enclosed space), these cues are expected to define category boundaries in association with the geometry of the task space. Conversely, when object landmarks are visible but displaced from any environmental landmarks, these cues are more likely to be associated with objects and to serve as prototypes that represent the mean locations of that object grouping. These category-association predictions for environmental versus object landmarks are supported by the goal-search behavior of different species that, in orientation processes, treat object landmarks (e.g., a rectangular array of four columns) just like environmental landmarks (e.g., the corners of a rectangular room) only when the geometric stability of the object cues is assured by proximity to environmental landmarks (i.e., a cylindrical wall; Lew, 2011). Although human object and place representations are not necessarily constrained to follow the same pattern that has been observed in other

animals, this framework provides a principled means of making testable predictions in humans. In the Discussion section below, we provide detailed structural–functional couplings for the possible dissociation between the two types of cue-based place-learning mechanisms.

For cases in which locations can be specified on a single dimension (e.g., azimuth), Huttenlocher et al.'s (1991) category-adjustment model captures the weighted relationship in an object–category association that combines fine-grain and categorical information:

$$E(R) = \lambda\mu + (1 - \lambda)p, \quad (1)$$

where $E(R)$ is the estimate of a target location, μ is the mean of the unbiased fine-grain representations (i.e., the actual target location), p is the mean of the unbiased categorical representations (i.e., the actual prototype location), and λ is the relative weight (or reliability) of fine-grain memory. Bias is estimated by subtracting the actual location from the estimated location, as follows:

$$E(B) = E(R) - \mu. \quad (2)$$

Huttenlocher et al. (1991) tested the category-adjustment model with a mark-a-dot task. Participants viewed a dot in a stimulus circle and reproduced the dot in an identical but empty response circle. With respect to the angular location of the dot, the model predicted a geometric bias derived from the four quadrants of the circle. As predicted, the dots were reproduced more inward in each category. The geometric categories were bordered at the horizontal and vertical axes of the circle, and geometric prototypes were observed near the 45° diagonals of the quadrants.

Furthering Huttenlocher et al.'s (1991) research on geometric bias in a circular domain, Fitting et al. (2005, 2007) examined whether external cues could function as prototypes. As in Huttenlocher et al.'s study, participants were asked to remember the location of a dot in a circular domain. In a stationary condition, the task circle was fixed in one orientation, and in a dynamic condition, the circle was rotated to different orientations during the test phase. Different groups saw different numbers of cues (three, one, or none) around the circular field. Whereas bias in the stationary condition reflected geometric prototypes, bias in the dynamic condition reflected cue-based prototypes.

Fitting et al. (2005, 2007) presented a cue-based fuzzy boundary (CBFB) function that predicts the effect of Prototype j (p_j) over multiple prototypes (p_k) for a given target (μ), with the probability

$$P(p_j|\mu) = \frac{\exp(-c|\mu - p_j|)}{\sum \exp(-c|\mu - p_k|)}. \quad (3)$$

Boundaries are inferred midway between two neighboring prototypes such that the prototype effects are equated at the boundaries. (The lower the value of c , the fuzzier the boundary.) This function computes a sigmoidal decline of bias near the boundaries. The CBFB version of the category-adjustment model is more flexible than the original version, in terms of the number and locations of prototypes. There is evidence that when human observers are immersed in a three-dimensional (3-D) environment and attempt to remember object directions, similar patterns of biases occur; specifically, geometric prototypes are found near $\pm 45^\circ$, relative to straight ahead, when the possible target locations are restricted to the front hemisphere (Haun, Allen, & Wedell, 2005). However, it is not yet known whether the two-category bias of the front hemisphere originates from a transient observer-based frame or is locked to the environment. We addressed this question in the present study. If the two categories are coordinated by a system that constructs the environment-centered frame, we would expect to see the biasing effect of the two categories even after the observer's heading within the environment changed due to a body rotation.

Category bias has also been examined in dynamic 3-D environments in which participants moved before indicating the remembered target locations (Fitting, Allen, & Wedell, 2008; Sargent, Dopkins, & Philbeck, 2011). In Sargent et al. (2011), participants first learned the locations of six targets while facing 0° (five of the targets were located between -45° and 90° , and one at -130°). Next, they were asked to rotate themselves in a swivel chair, while blindfolded, to face certain remembered target locations (at -45° and 90°) or to return to the remembered 0° heading. From these test headings, they then indicated the remembered locations of all of the targets. Thus, remembered target directions served as orientation cues for the blindfolded participants. In the analyses of targets located in the front hemisphere, no bias was found when the data were plotted relative to the training heading; that is, the blindfolded and rotated participants showed no geometric bias, or no association between their target memory and the geometry of the cylindrical arena. When plotted relative to the test headings, however, the data did show a two-category bias (-48° and 55° prototypes) and a dynamic boundary centered on 0° relative to the participant's heading after the body rotation. Since the orientation cues and test headings were both aligned with the dynamic 0° boundary, however, it was not clear whether the resulting category biases were caused by the orientation cues or the test headings. In another study involving a dynamic 3-D environment (Fitting et al., 2008), participants estimated one object location from several entrances along the cylindrical wall. Either two or four picture cues were provided equidistant from each other on the wall. The cues were named "north" and "south" in the two-cue condition, and "north," "south," "east," and "west" in the four-cue condition. The target was

hidden 47.4° counterclockwise from "north." Participants learned the target location by being led to the location, and subsequently they estimated the remembered target location by walking in a straight line from the entrance locations to the estimated location. Consistent with the CBFB prediction for a 2-D circular field, cues served as prototypes in the 3-D cylindrical domain. The target between northwest and west was misremembered clockwise toward the north cue in the two-cue condition, but counterclockwise toward the west cue in the four-cue condition. The magnitude of this bias increased when the memory load and delay interval increased. These 3-D bias profiles have shown that both environmental geometry and external cues are used to establish frames of reference that can bias location judgments. However, a few important questions remain unanswered: Do the initial coarse-grain representations of an environment (e.g., bisection of an environment) actually form the basis for spatial categories when an observer is moving in the domain? Can object landmarks also play a role in establishing the environment-centered frame and create different spatial categories? We address these questions in the present article.

We tested for three sources of bias: the geometry of the environment, object landmarks, and environmental landmarks (i.e., doors). Each participant was seated in the center of a cylindrical chamber and tested for short-term memory of objects presented at 32 azimuths, dispersed symmetrically along the perimeter of the space (see Fig. 1). The symmetrical object dispersion was designed to focus on localization bias, which is maximized with distance from the effective cue and then declines with further distance as it approaches the neighboring category.

In one condition, the task environment provided no external cues other than the geometric shape of the domain (i.e., a cylinder with vertical or horizontal reference axes).

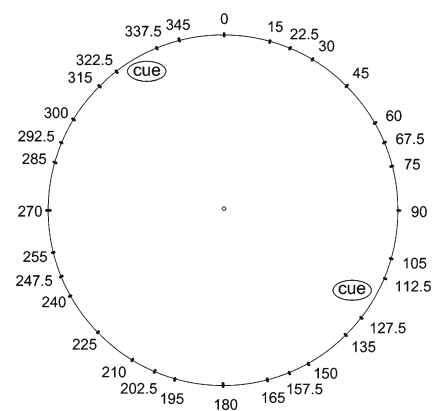


Fig. 1 Experimental setup. The circle represents the floor of the task cylinder, in which each participant was seated at the center. The 32 target locations are marked with bold dots. The "Cue" labels at 120° and 330° indicate either two objects, in the object-cue condition, or two doors, in the door-cue condition

This situation is analogous to the 2-D circular domain that has been studied in past work, but never fully implemented in a 3-D domain (Fitting et al., 2005, 2007; Huttenlocher et al., 1991). It remains unclear how many distinct categories are present when targets are evenly distributed around the periphery of the environment. One possibility, consistent with what has been observed in a fixed 2-D circle, is that the enclosing space would be divided into four quadrants by two orthogonal axes crossing at the center (see Fig. 2a). Another possibility is that the body’s sagittal axis would be sufficiently salient and dominant (perhaps because of the pattern of hemispheric specialization in the cortex for processing contralateral inputs) that the environment would simply be bisected into two categories based on the observer’s initial observation point during learning (see Fig. 2b).

The no-cue condition also provided the opportunity to observe whether the categories would be laid out symmetrically with respect to the front and rear. The front–rear symmetry hypothesis holds that geometric prototypes would arise

at the centers of all categories (45°, 135°, 225°, and 315° under the four-category hypothesis, and 90° and 270° under the two-category hypothesis). In each category, subcategories on the participant’s left and right would be split by the effective prototype. Target locations were predicted to be biased clockwise in the left subcategories, and counterclockwise in the right subcategories (i.e., toward the four or two geometric prototypes). Since the participant’s vision was centered at a heading of 0°, we also considered the possibility that the front and rear spaces would be treated differently in the category-association process (Franklin, Henkel, & Zangas, 1995). The front–rear asymmetry hypothesis holds that the categories would be asymmetrical between front and rear, and symmetrical between left and right.

Besides the no-cue condition, we also included two cue-based conditions (object and door cues), through which we sought to examine whether the categorical structure of an environment (i.e., four quadrants or simple bisection) remains in memory and organizes place representations even after observers move, and whether object and environmental landmarks can both create spatial categories when used for reorientation. First, we were alert to the possibility that location judgments of our cue-based groups would reveal the influence of the environment-centered reference frame. Comparing two particular external cues in our design allowed us to investigate this possibility. Two cues were placed 30° from the nearest cardinal direction: the 330° cue relative to 0° (the study heading), and the 120° cue relative to 90° (see Fig. 1). The front–rear asymmetry hypothesis predicted that the environment-centered frame would attenuate the effect of the front cue (330°) more than the effect of the rear cue (120°), independent of test headings. In this case, we expected to see the cue effect more clearly around 120° than around 330°. Second, different groups were provided with either object or door cues near the cylindrical wall. This allowed us to control for the stability of the cue locations. If the stability is a major determinant in shaping reference frames, there should be no significant difference in bias caused by the object and door cues. In contrast, if the type of landmarks predetermines their function, the door cues should produce different spatial categories in association with the environmental geometry, whereas object cues should more likely play roles in defining category prototypes. In addition, Sargent et al.’s (2011) finding of a bias that rotated with different cue–observer alignments led us to examine whether the bias pattern would follow external cues, test headings, or both when the two factors were misaligned. Our cue-based groups had two external cues (i.e., two doors or two objects) and eight test headings at different directions. If test headings shape localization frames, the cue effect would be different in the left and right spaces after a body rotation to the test heading.

The function of dot cues observed in Fitting et al.’s (2005, 2007) dynamic 2-D domain predicted clockwise errors on the

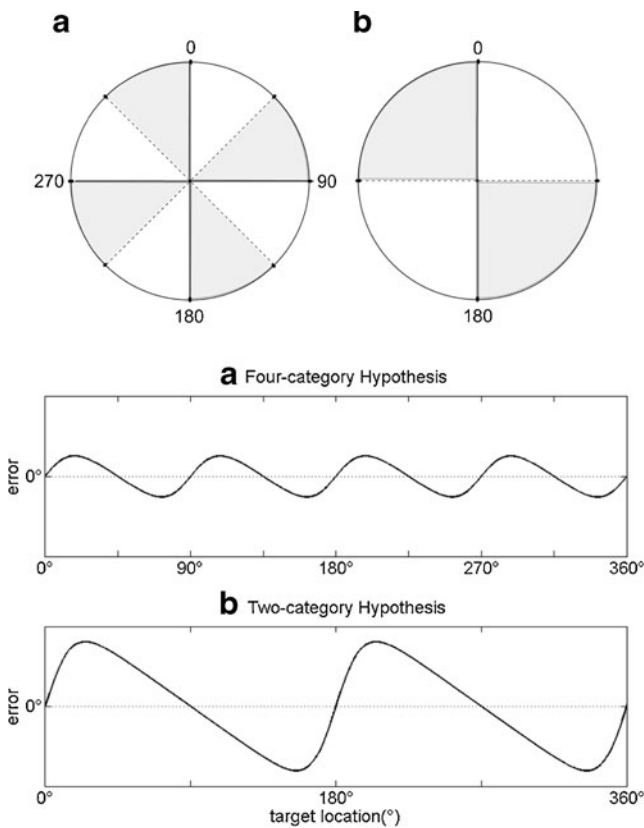


Fig. 2 Potential categorical divisions of our 3-D environment. The pairs of white and gray sectors represent the geometric categories of the four-category hypothesis, in Circle A, and the two-category hypothesis, in Circle B, assuming the front–rear symmetry hypothesis. The bold axes with direction labels represent geometric boundaries, and the dotted axes represent geometric prototypes. The two bottom panels A and B show the bias functions predicted in circles A and B, respectively. The difference in bias size between panels A and B depicts that the use of more prototypes (i.e., four as opposed to two) can potentially lead to higher accuracy

left side of our object cues and counterclockwise errors on the right (see Fig. 3). According to the category-association prediction, these cues indicate cue-based prototypes in association with a cluster of test objects. Cue-based boundaries were expected to lie midway between the two cues (45° and 225°). That is, the two cue-based categories were predicted to be identical semicylinders bounded at 45° and 225° , with prototypes $\pm 75^\circ$ from the 45° boundary and $\pm 105^\circ$ from the 225° boundary.

With the door-cue condition, we further asked whether or not environmental landmarks have a distinct effect on shaping reference frames. Consistent with the category-association prediction, if the doors are treated as boundaries when spatial categories are generated in association with the geometry of the environment, errors would be expected to fall counterclockwise on the left side of the

door cues and clockwise on the right (see Fig. 3). In addition, if both types of cues (door and object) function as boundaries and reflect cue–geometry associations, this would support the view that not environmental geometry per se, but geometric stability, determines the shape of the cue-based reference frame.

Method

Participants

A group of 45 participants, ranging in age from 18 to 22, were recruited from the Psychology Department's subject pool at George Washington University. We excluded the data for one participant in the no-cue condition who produced outliers (two standard deviations below or above the mean error at each target location) in more than half the estimates. The final sample comprised 14 participants in the no-cue condition, and 15 participants in the object-cue and door-cue conditions.

Materials

The cylindrical chamber, 3.75 m in diameter and 2.55 m in height, was enclosed by a black polyester curtain. For participants in the no-cue condition, no external cues were provided in the cylinder. For those in the two cue-based conditions, external cues were provided during the entire experiment. The external cues were a coat tree and a lamp in the object-cue condition, and two doors (curtain gaps) in the door-cue condition. Upon first entering the chamber, the object-cue group was asked to take the blindfold, which was hung on the lamp, and put their belongings on or against the coat tree. The door-cue group was guided into the cylinder through one of the two gaps in the curtain. At this point, they were told that the cylinder had two doors.

Participants were seated in a wooden chair that was affixed to the top of a rotation platform that added approximately 18 cm to the height of the chair. The extent of rotation, peak velocity, and acceleration profile of the rotation platform were controlled by a desktop PC. The four target objects were a 2×4 in. board ($5 \times 10 \times 92$ cm), a wooden dowel (approximately 1.5 cm in diameter), a broom and a mop. They were vertically placed on separate stands, and varied from 90 to 160 cm in height. Each object was placed approximately 1.85 m from the participant. Participants used a pointer to indicate their estimates of the target directions (see Sargent, Dopkins, Philbeck, & Chichka, 2010, for details of the pointing apparatus). The “front rod” of the pointer was 18 cm long, and attached to the top of a bicycle rim, which horizontally enclosed the

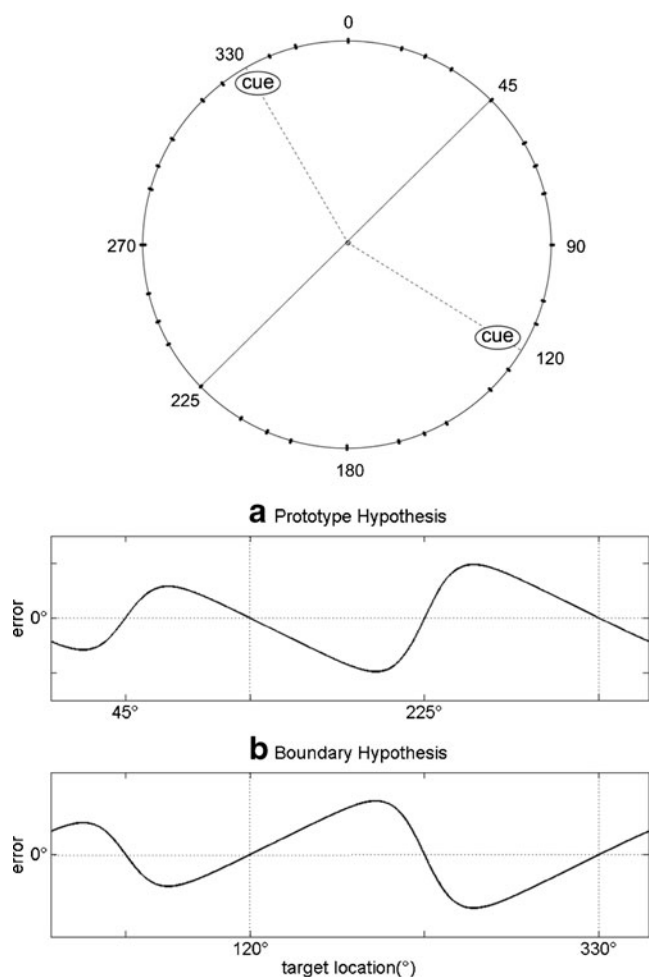


Fig. 3 Different categories defined according to the cue function in our 3-D environment. When the cues function as prototypes, two semicylindrical categories are bordered at the segment that connects angles of 45° and 225° . When the cues function as boundaries, two categories are bordered at the dotted lines that connect the angles of 120° and 330° . The two bottom panels A and B show the bias functions predicted for the cues acting as prototypes and boundaries, respectively

participant at the level of the chair’s armrests. A 9-cm rod (the “back rod”) was attached and aligned with the front rod, and indicated a point 180° from the aiming direction. This pointing apparatus allowed the chair and the pointer to share a common axis of rotation (the observation axis) that was located within the participant’s body. In using the pointer, participants put one hand on the front (aiming) rod and one hand on the back (guiding) rod, and looked directly back and forth by turning their head and torso. Thus, we assumed no significant difference in pointing responses for the front and rear target locations due to the pointer rotation axis being offset from the egocentric observation axis (Philbeck, Sargent, Arthur, & Dopkins, 2008).

Design

The four targets occupied three quadrants in all study phases, and either three or four quadrants in all test phases, with one exception of two test quadrants. The four targets were dispersed to require immersive 3-D representations in all trials (see Tommasi, Chiandetti, Pecchia, Sovrano, & Vallortigara, 2012, for further discussion of local and global representations). In addition, the multiple targets were expected to increase memory load and the bias effect (Fitting et al., 2008).

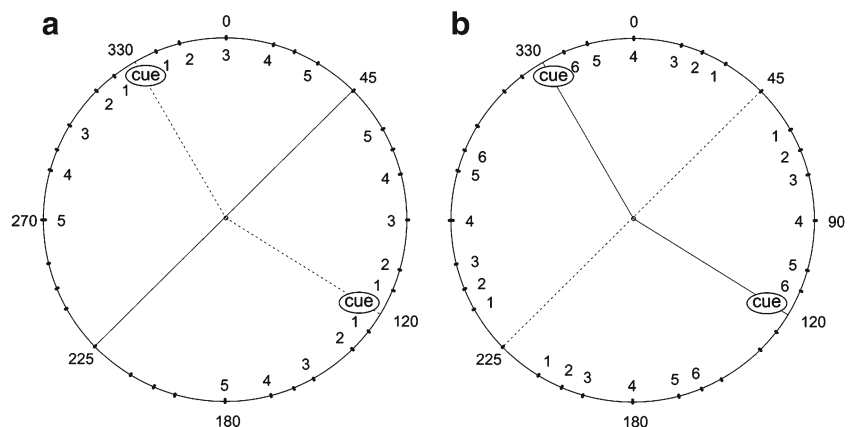
The experiment consisted of nine trials. Each trial was composed of one study and two test phases. Participants made seventy-two location judgments in total. In each test phase, the target objects were tested in random order. Over the course of the experiment, 28 target locations were tested twice and four target locations (0°, 90°, 180°, and 270°) were tested four times. The 32 target locations were symmetrically dispersed in the two semicylinders split by the 0° and 180° geometric boundaries, and the two semicylinders split by the midpoints (45° and 225°) of the external cues (see Fig. 4). Specifically, each cue-based subcategory contained target locations at five angles of 7.5°, 15°, 30°, 45°, and 60° from the nearest cue, and at

six angles of 15°, 22.5°, 30°, 45°, 60°, and 67.5° from the nearest midpoint.

Participants faced 0° during the study phases and were rotated for each test phase. For the cue-based groups, the test heading was randomly sampled from the set of eight headings (40°, 50°, 100°, 140°, 220°, 260°, 280°, and 350°). This was to see the effect of the external cues as prior 2-D studies have observed cue-based bias on a dynamic task circle but geometric bias on a stationary task circle when external cues were equally present (Fitting et al., 2005, 2007). In addition, the misalignment of the test headings and the cue locations allowed us to test if there is a bias that rotates with the observer. In the no-cue condition, however, participants were rotated to one of the above headings and back to 0°. The constant heading before and after rotations made the geometric cues available for both the study and test phases. In addition, the passive rotations away from and toward 0° were intended to activate the geometric cues more strongly for reorientation.

Note that in our methodology, the test headings were not equivalent between the no-cue and cue-based conditions. Accordingly, we considered two alternative no-cue conditions that matched the rotation procedure used in the object-cue and door-cue conditions (that is, participants were not rotated back to 0° before responding). In the alternative conditions, observers were rotated to the test headings used in the cue-based conditions and made location judgments while updating rotations (Case 1) or ignoring rotations (Case 2). Case 1 was not equivalent to our cue-based conditions, in that the cues (geometry) were unavailable during the test phases. In Case 2 these cues were available, but conflict was introduced between the real and imagined headings. Prior studies have shown that location judgments are better (in terms of both accuracy and response time) at real viewpoints than at imagined viewpoints (Farrell & Thomson, 1998; May, 2004; Waller, Montello, Richardson, & Hegarty, 2002). Thus, we rotated the no-cue group once more back to 0° to remove the

Fig. 4 Symmetry of the target locations in our 3-D environment. Each subcategory contains five distances of 7.5°, 15°, 30°, 45°, and 60° from an abutting cue (the labels “1” to “5” in Circle A), and six distances of 15°, 22.5°, 30°, 45°, 60°, and 67.5° from an abutting midpoint between the cues (labels “1” to “6” in Circle B). This symmetry generates four common distances (15°, 30°, 45°, and 60°) from the abutting cue and the abutting midpoint



conflict. In sum, the different rotation procedures were expected to make the cue-based and no-cue conditions more equivalent, in that the primary cues of interest—external cues in the cue-based conditions and environmental geometry in the no-cue condition—remained at fixed locations during both the study and test phases.

Experimental procedure

Participants were tested one at a time. Participants were blindfolded after they sat at the chair on the rotation platform while the experimenter placed the target objects in the chamber. During the study phase, participants removed the blindfold and studied the target locations for 8 s. Participants were blindfolded while the experimenter rotated them to a given test heading and removed the target objects from the chamber. The retention interval between the study phase and the first test phase was less than 2 min.

Participants in the two cue-based conditions were rotated to the same test headings. In the first rotation (Rotation 1), blindfolded participants were rotated clockwise from 0° to Test Heading 1. They removed the blindfold and pointed to the estimated target locations. In the second rotation (Rotation 2), blindfolded participants were rotated counterclockwise from Test Heading 1 to Test Heading 2. They removed the blindfold and estimated the target locations once more. For the next trial, participants blindfolded themselves and experienced Rotation 3 back to 0° by the shortest path.

In the no-cue condition, blindfolded participants experienced Rotation 1A clockwise to Test Heading 1, determined in the same way as for the cue-based groups, and Rotation 1B back to 0°. Participants were informed that they had been reoriented to face the study heading. Participants removed the blindfold and estimated the target locations. They again experienced Rotation 2A counterclockwise to Test Heading 2, as in the cue-based groups, and Rotation 2B back to 0°. They were again informed of their reorientation to 0°. Participants removed the blindfold and estimated the target locations once more. For the next trial, blindfolded participants experienced Rotations 3A and 3B back to 0°. Rotation 3A corresponded to the cue-based Rotation 3 in terms of both direction and distance.

Results

For the pointing response to a given target location, the *angular estimate* was the angular distance clockwise from the study heading (0°) to the pointing direction. The *angular error* was the difference between the angular estimate and the actual direction. Positive angular error reflected clockwise

error. Several participants did not complete the last trials of the experiment. The data were 82.84 % complete in the no-cue condition, 86.57 % complete in the object-cue condition, and 80.28 % complete in the door-cue condition. We did not replace the missing data. Outlying data points were omitted if they were two standard deviations below or above the mean angular error at each target location within each condition. This protocol omitted 6.47 % of the no-cue data, 7.49 % of the object-cue data, and 7.04 % of the door-cue data.

We conducted repeated measures analyses of variance (ANOVAs) on the entire data set of all three conditions involving participants' multiple estimates at each of the 32 target locations. As is shown in Table 1, this analysis showed no interaction between cue condition and test heading, but there was a significant interaction of cue condition and target location. Similarly, separate repeated measures ANOVAs on the entire data set of each condition showed no effect of test heading in the no-cue and door-cue conditions; no interaction between test heading and target location emerged in any of the three conditions, but we did find significant main effects of target location in all three conditions. In order to test whether location judgment errors differed across the 32 target locations, we used different data sets that comprised the 32 mean estimates of each participant for the 32 target locations (collapsing over test headings). Repeated measures ANOVAs on this data set showed a significant main effect of target location and a significant interaction of cue condition and target location. Post-hoc analyses showed that the target location effects differed significantly between the no-cue and door-cue conditions [$F(31, 668) = 2.41, p < .001$]. The effect of target location in the object-cue condition did not differ significantly from either the no-cue condition or the door-cue condition. To look at the within-subjects effect of the target location without considering the between-subjects effect of the cue, repeated measures ANOVAs were conducted separately for each condition. The effect of the target location was significant for the no-cue condition and the door-cue condition, and was marginally significant for the object-cue condition. On the assumption that shifts in bias directions are informative about the underlying frames of reference (e.g., the locations of prototypes and boundaries), the mean error at each target location was tested for significance. We found significant mean differences for 14 of the 32 target locations in the no-cue condition, for two target locations in the object-cue condition, and for one target location in the door-cue condition. Figure 5 shows the significant and borderline significant mean differences in the three conditions (filled dots). The no-cue data revealed a larger number of significant and borderline differences (16 target locations) than did the object-cue data (two target locations, $z = 3.89, p = .0001$) and the door-cue data (four target locations, $z = 3.24, p < .001$).

The CFBF version of the category-adjustment model was adopted to fit the 32 angular errors averaged at each target location. We used a simplex method to minimize the squared

Table 1 Results of analyses of variance (ANOVAs) on pointing errors

Bias Source	No-Cue Data (<i>dfs</i>) <i>F</i> value	Object Data (<i>dfs</i>) <i>F</i> value	Door Data (<i>dfs</i>) <i>F</i> value
Test Heading (H)	(7, 2200) 1.73		
Target Location (L)	(31, 2202) 5.22***		
Cue Condition (C) × H	(14, 2200) 1.66		
C × L	(62, 2202) 1.86***		
H × L	(31, 2199) 0.62		
C × H × L	(62, 2199) 0.55		
H	(7, 698) 1.42	(7, 781) 2.02*	(7, 722) 1.5
L	(31, 699) 6.49***	(31, 783) 2.22***	(31, 722) 2.34***
H × L	(31, 698) 0.7	(31, 781) 0.52	(31, 722) 0.6

ANOVAs on the data set that contains all three conditions are indicated across three cue columns. ANOVAs on separate data sets for each condition are indicated under each cue-data column. * $p < .05$. *** $p < .001$

difference between the predicted and observed values. Parameters consisted of λ , c , and the values of the prototypes. In addition, two virtual prototypes were assumed, following

Fitting et al. (2005, 2007), in response to the cyclic character of the data (e.g., 0° and 360° index the same angular direction). The two virtual prototypes were placed 360° above the lowest

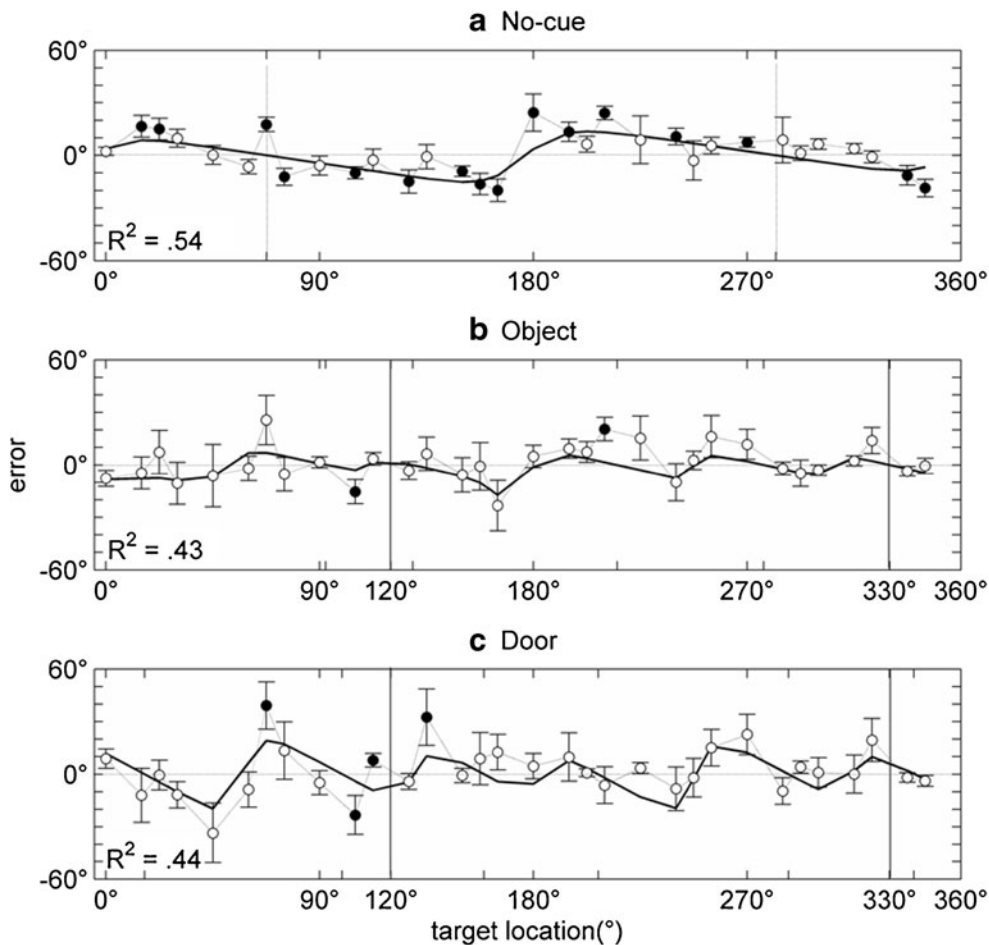


Fig. 5 Two-, five-, and six-category fits of the category-adjustment model (bold function lines) to the no-cue data (a), the object-cue data (b), and the door-cue data (c), respectively. Two cues in Conditions B and C are indicated at 120° and 330° (vertical guidelines). The model-inferred prototypes are indicated at 68° and 282° (vertical dotted lines) in Condition A

and are marked at various places on the horizontal axis in Conditions B and C. The 32 filled and open circles on the dotted lines indicate the mean angular errors at each target location. The filled circles represent those errors that differed from zero significantly or with borderline significance, and the error bars are the standard errors of the means

prototype and 360° below the highest prototype. They were treated as fixed variables and were not included in the parameter set. In order to make sure that the solutions we found were the best solutions possible—that the minima that we found with our optimization analyses were as close as possible to global minima—we tried a range of starting values for parameters.

For the no-cue group, the model fit supports the two-category hypothesis (see Fig. 5), as the proportion of variance accounted for was not significantly increased when four as opposed to two categories were included in the model [$F(2, 25) = 3.13, p > .05$] (see Table 2). Second, the model fit supports the front–rear asymmetry hypothesis. The model-inferred prototypes at 68° and 282° were pulled toward the study heading (0°). The boundaries were inferred as being at 175° and 355°, midway between the two model-inferred prototypes. Notice the proximity of 355° and 175° to the angles of 0° and 180°, which divide the observer's left and right spaces. Thus, we took the salient angles of 0° and 180° to function essentially as geometric boundaries.

The mean errors were consistent with the model interpretation in all subcategories (see Fig. 6). The mean errors were significantly positive in the right–front [$t(13) = 2.98, p = .01$] and in the left–rear [$t(13) = 4.03, p = .001$] subcategories, and significantly negative in the right–rear subcategory [$t(13) = -3.17, p < .01$]. The mean error was not significant in the left–front subcategory. The absolute mean error was significantly greater in the rear than in the front [$F(1, 54) = 4.13, p = .05$]. We suggest two possible

explanations for the greater bias in the rear. First, rear targets were on average farther from an effective cue because the geometric prototypes were asymmetrically situated within the categories, and second, fine-grain memory was poorer in the rear because the rear was more distant from the center of vision and behavior. This account also explains the greater bias around 180° than around 0°. Likewise, correct estimates (zero error) were much more frequent at 0° than at 180°.

In the object-cue condition, the six-category version of the model accounted for more variance than did the two-category version [$F(4, 23) = 2.91, p < .05$] or the four-category version [$F(2, 23) = 3.1, p = .06$], suggesting the utilization of both geometric and cue-based frameworks (see Table 2). We also tested for the five-category version, and found no significant increase in the proportions of variance explained by six as opposed to five categories [$F(1, 23) = 4.28, p > .1$]. We were alert to the possibility that as the number of parameters increases, significant model fits could be obtained by chance (i.e., by fitting noise). In the interpretation of our cue function, however, we used the six-category version, which was theoretically motivated to explain both geometric and cue-based frames of reference.

Inconsistent with the cue function in a 2-D domain, one of the cues appeared to function as a boundary. In the rear part of the cylinder, the model inferred a boundary near the lamp cue at 120°. A significant mean error was made in a predicted direction at 105° ($M = -15.38, SD = 26.8, p = .04$), supporting the boundary effect of the 120° cue (see Fig. 5). In the front part of the cylinder, the 330° cue was a similar

Table 2 Parameter values and fit indices for the CBFB version of the category-adjustment model

Model/ Condition	Parameter								R^2
	λ	c	$p1$	$p2$	$p3$	$p4$	$p5$	$p6$	
Two-Category									
No cue	.8	.07	67.56	282.06					.54
Object cue	.91	.06	59.44	309.6					.17
Door cue	.47	.07	165.98	315.02					.12
Four-Category									
No cue	.69	.09	58.37	92.02	249.84	302.12			.63
Object cue	.81	.08	3.15	98.53	266.5	346.46			.3
Door cue	.7	.12	124.53	195.85	293.09	347.8			.22
Five-Category									
Object cue	.7	.22	92.45	129.2	215.21	276.98	330.05		.43
Door cue	.62	.13	0	116.23	196.7	293.91	338.25		.26
Six-Category									
Object cue	.49	.16	26.37	89.4	134.92	220.91	279.29	344.14	.45
Door cue	.27	.15	16.27	99.48	159.08	207.31	287.45	340.27	.44

The bold type indicates the best-fitting version for each condition. λ , weight of fine-grain memory; c , sensitivity parameter; $p1$ – $p6$, prototypes; R^2 , proportion of variance explained.

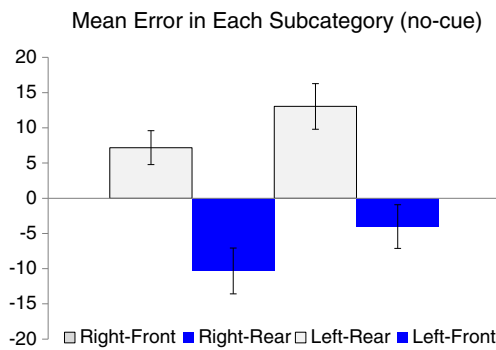


Fig. 6 Histogram showing the mean error in each subcategory of the no-cue condition. The error bars are the standard errors of the means. Left–right and front–rear were differentiated according to the boundaries and prototypes, respectively, given by the model. The absolute mean errors were 5.6 in the front and 11.69 in the rear

distance from the model-inferred boundary at 312° and the model-inferred prototype at 344° . Mean errors were not significant near the 330° cue, and were relatively small between the 330° cue and the study heading (0°).

The object-cue data implied that participants relied on the geometric frame in addition to the cue-based frame. The model-inferred boundary at 178° was accompanied by a significant mean error at 210° ($M = 20.4$, $SD = 25.94$, $p < .01$). The model-inferred prototype at 89° was accompanied by a significant error at 105° ($M = -15.38$, $SD = 26.8$, $p = .04$). These results support the view that the geometric frame established during the study phase played a role in the object-cue condition.

Finally, in the door-cue condition, the six-category version of the model explained significantly more variance than did the two-category version [$F(4, 23) = 3.26$, $p < .05$], the four-category version [$F(2, 23) = 4.47$, $p < .05$], and the five-category version [$F(1, 23) = 4.28$, $p = .01$], again suggesting the utilization of both geometric and cue-based frameworks (see Table 2). Consistent with the category-association prediction that architectural structures such as doors would construct different categories within the geocentric frame, in the rear part of the cylinder, a boundary was inferred near the 120° cue. The mean error showed a positive trend at 135° ($M = 32.53$, $SD = 62.33$, $p = .06$) and a negative trend at 105° ($M = -23.23$, $SD = 41.26$, $p = .06$), supporting the boundary effect of the 120° cue (see Fig. 5). At the nearest target locations of 112.5° and 127.5° , the mean error was smaller, but showed an inconsistent trend. In the front part of the cylinder, the 330° cue was a similar distance from the model-inferred boundary at 340° and the model-inferred prototype at 314° . The means of the nearby target locations were not significantly different. The results for the door-cue condition were consistent with the results for the object-cue condition in that the function of the 330° cue was unclear whereas the 120° cue appeared to act as a boundary. This supports the

idea that the study heading (0°) structured the geometric frame and affected memory of moving participants in both object- and door-cue conditions.

The door-cue data also implied the participants' utilization of the geometric frame. In contrast to the case with the object-cue data, however, the model-inferred boundary at 183° was not accompanied by a significant mean error. The model-inferred prototype at 99° was accompanied by a significant error at 67.5° ($M = 39.2$, $SD = 52.08$, $p = .01$).

Discussion

In this study, we asked whether the categorical structure of place representations constitutes an environmental frame that can be used by moving observers, and whether environmental and object landmarks can both play a role in forming spatial categories. Our findings suggest that the biasing effects of environmental geometry and external cues differ between 2-D and 3-D domains.

In our no-cue condition, the geometric categories were bipartite; in prior 2-D studies, the geometric categories had been quadripartite. This difference suggests that the four cardinal directions have equivalent valences on the 2-D surface, and not in the 3-D space. In addition, the two geometric prototypes were pulled forward in the left and right categories. This differed from the 2-D case, in which geometric prototypes have typically been observed near the center of each quadrant (Fitting et al., 2005, 2007; Huttenlocher et al., 1991). The unequal valences in our immersive situation show the pivotal roles of vision and self-motion information in integrating perceptual cues (in this case, environmental geometry) into the environment-centered localization system.

Our findings constitute an advance over the results of Haun et al. (2005). First, Haun et al. looked at the front hemispace only; accordingly, they could not address the question of two versus four geometric categories. In contrast, we looked at the full cylinder, and found that the 3-D geometric frame was more consistent with two categories. Second, we could answer the front–rear asymmetry question. Geometric prototypes were located near categorical centers (near -46° and 33°) in Haun et al.'s hemispace, but off categorical centers (near -78° and 68°) in our immersive situation. Third, we observed the bisecting framework in all three conditions, even when participants rotated before responding. This suggests that two-category representations of an environment form a fundamental framework that supports place representations.

One concern in our methodology is that the cue manipulation was confounded to some degree with body rotation, in that the participants' viewpoint was constant in the no-cue condition, but rotated during judgments in the two cue-based

conditions. This potentially complicates the interpretation of the biases that we observed. Importantly, however, our results showed that the body rotation in our cue-based conditions (i.e., test heading) had no role in generating the reference categories. The cue-based biases were independent from the test headings. Another potential concern is that category information (e.g., via the door or object cues) could have been directly accessed from the environment during test phases, rather than being stored in memory. Although this was indeed a possibility, the blindfolded body rotations in the door- and object-cue conditions required our participants to remember the cue configuration and its relation to the environment for successful reorientation. In addition, remembered cue–object pairing was required in order for the cues to support location judgments of the removed objects. If participants could not store any direct or indirect connection between the cue and the object during study phases, the category information, though perceptually available, could not be used to localize the removed objects. Thus, we contend that the most important aspects of the category associations were indeed stored in memory.

Interestingly, in the object-cue condition, the rear cue appeared to function as a boundary. This was inconsistent with the cue function in a 2-D domain (Fitting et al., 2005, 2007). The category-association assumptions that we introduced to explain unstable and stable external cues provide a prediction for the differing functions of the cues. In the 2-D case, the entire domain (both cues and target) was simultaneously visible, but the geometric frame was undefined after the task circle was rotated. Thus, the dot cues could be associated with the object distribution only, and so functioned as prototypes. In the 3-D case, however, the two object cues were stably positioned near the wall, and thus could be associated with the environmental geometry in the process of reorientation. In addition, geometric bias did not operate in the dynamic 2-D domain, but did operate in our 3-D domain. In our 3-D task, the cue effect, which was clear at 120° but less obvious at 330° (–30°), suggests that the environmental geometry was mapped into the environment-centered system and attenuated the cue-based bias to a greater degree in the front than in the rear, independent of the participants' test headings.

In demonstrating that an external cue functioned as a boundary in an immersive 3-D domain, our results differ from those that Fitting et al. (2008) observed in a 3-D domain (in which their cues functioned as prototypes). In Fitting et al. (2008), the whole domain (both cues and target) was viewed from perspectives outside the configuration. Accordingly, the cue–object association was more efficient than the cue–geometry association. In our experimental setup, however, the viewer was inside the configuration. Thus, the cue–geometry association was required for reorientation after each rotation to different test headings.

The cue–geometry association also provides an explanation for the results of Hutcheson and Wedell (2012), in which distal cues served as boundaries in a virtual environment (VE). One target and two external cues (north and south or east and west) were studied in a map on a computer screen. The external cues functioned as boundaries when tested in the VE, but as prototypes when tested on the map. Hutcheson and Wedell suggested that observers are flexible and influenced by the retrieval context in using category information. In addition, the category-association prediction explains that, whereas the cue–geometry association was developed while observers were navigating and reorienting in VE, the cue–object association blocked the cue–geometry association during the map retrievals when observers did not need to process an enclosing environment.

Finally, in our door-cue condition, the door at 120° showed a clear tendency to function as a boundary. The boundary function of both the object and door cues supports Lew's (2011) expectation that stable object landmarks can structure frames of reference similarly to the way that environmental landmarks do. This was probably part of the category-association tendency, where cues are conjoined into the environment-centered framework when used for reorientation. The amount of bias around the 120° cue was significantly greater in the door than in the object condition. This suggests that the cue–geometry association is stronger for environmental than for object landmarks when both types of landmarks have equivalent stability.

In sum, all three conditions suggest that the initial coarse-grain representations of environmental geometry coordinate and bias remembered object locations when observers construct place representations that extend beyond the field of view. The two-category frame supports rapid processing of an immersive environment, and thus likely serves as a fundamental construct of the environment-centered system during navigating and learning an environment. Henke (2010) suggested that the hippocampus accomplishes place representation automatically, even within a single trial. Our behavioral data of coarse-grain place representations are consistent with the idea that the two-category frame constitutes a default organizational tendency used by the hippocampal system during place learning and recognition. In this view, cue–object associations may engage both a rapid, hippocampally mediated system (in this case, accomplishing episodic cue–object binding in a single trial), and a slower learning system mediated by the basal ganglia and the cerebellum (in this case, gradually establishing habits or procedural memories). In our study, both door and object cues showed the cue–geometry association, suggesting that both types of cues can create different categories in the environment-centered frame.

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