Boundaries in Spatial Cognition: How They Look is More Important than What They Do

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ABSTRACT

Typical boundaries (e.g. large walls) strongly influence neural activity related to navigation and representations of spatial layouts. Typical boundaries are also a major aid to reliable navigation in young children and non-human animals. One hypothesis places this as a function of the walls being boundaries, defined by proponents as obstacles to navigation. An alternative hypothesis suggests that this is a function of visual covariates such as the presence of large 3D surfaces. Using immersive virtual reality, we dissociated whether walls in the environment were true boundaries (i.e., obstacles to navigation) or not (i.e., visually identical but not obstacles to navigation), or if they were replaced with smaller objects. 20 adults recalled locations of objects in virtual environments under four conditions: *plywood*, where a visual wall coincided with a large touchable piece of plywood; *pass through*, where the wall coincided with empty space and participants could pass through it; *pass over*, where the wall was underneath a transparent floor, and *cones*, where there were traffic cones instead of walls. Spatial coding behavior (biases, precision) changed only as a function of visual changes to the items (i.e., large 3D surface vs. small object). This suggests that variations in spatial coding are more closely linked to the visual properties of environmental layouts than whether they function as true boundaries.

Keywords: boundary; allocentric; spatial memory; navigation; virtual reality.

1. Introduction

Spatial memory and navigation are among the most important and widely-shared cognitive activities that humans and other organisms perform. In the study of spatial cognition, there has been wide interest in differences that appear when presenting typical boundaries versus typical non-boundaries (also called landmarks, beacons, or signs) in the environment. These differences are evident in a wide variety of effects, including on learning (e.g. Doeller & Burgess, 2008), neural representations (e.g. Ito, Zhang, Witter, Moser, & Moser, 2015), and systematic biases (e.g. Newcombe & Liben, 1982). This lends insight into the mechanisms of spatial cognition; it suggests that boundaries in natural scenes play a crucial role in how we and other animals represent and navigate the world around us (Lee, 2017).

To test these differences, research has frequently compared boundaries that function as obstacles to navigation versus non-boundaries that similarly mark an area but allow navigation across them. Typically, these have been ecologically valid stimuli representing commonly-encountered examples, such as boundary exemplars like large walls versus non-boundary exemplars like traffic cones (e.g. Mou & Zhou, 2013) or flat markings (Lee & Spelke, 2011). However, not only are traffic cones and flat markings less physically relevant for navigation than big walls, they are also visually very different. This means that a traffic cone and a large wall vary along at least two factors: their physical affordances and their visual appearance. Thus, such stimuli lack experimental controls that would let us conclude exactly which differences influence results. To achieve better experimental control, we make use of recent technological developments to present people in immersive virtual reality with a set of walls that they can move their hand through with no resistance whatsoever (‘pass through’). We have another condition that looks exactly the same but uses a piece of plywood to block movement, creating a true boundary (‘plywood’), a third that puts the walls under a

translucent floor (‘pass over’), and a fourth with some traffic cones instead of walls (‘cones’). Our conditions therefore allow us to make a two-factor conceptual distinction for testing.

We define a “true boundary” as an item that functions physically to impede navigation, and does so to an extent that efficient navigation must consider it (i.e. excluding small inconveniences like walking around a traffic cone). We define “visual covariates” as the typical visual features of items that qualify as boundaries, such as their size, the presence of extended 3D surfaces, and so on. As we will see later on, these definitions make the following text the easiest to understand and the connection to the literature the clearest. Table 1 illustrate how these are dissociated and gives further terminology for the different categories.

Table 1. Definitions of major terms.

		Is a **True boundary** (i.e. is an obstacle to navigation)	
		Yes	No
Has Boundary **Visual Covariates** (e.g. has an extended 3D surface)	Yes	*Boundary Exemplar* e.g. walls of a building, cliff faces. Here, the "plywood" condition.	*Visual Barrier* e.g. a hologram of a stone wall. Here, the "pass through" and "pass over" conditions.
	No	*Mere Boundary* e.g. an acrylic (Plexiglass, Perspex, Lucite) wall – or even better, a wall that cannot be seen in any way at all. Omitted here for practical considerations.	*Non-Boundary Exemplar* e.g. traffic cones, small plants, flat markings on the ground. Here, the "cones" condition.

Note. In this treatment, we set aside social effects and metaphorical uses of the word "boundary". For example, a single line of police tape in this treatment would be considered a non-boundary exemplar because it does not actually have much physical action to impede navigation. The metaphorical "boundaries" drawn on a basketball court are also non-boundary exemplars. These additional nuanced effects (i.e. the functions a social cue that something should not be navigated across) are left for future work, as this allows us to engage more directly with comparative work in species without the same kinds of clear social and metaphorical functions (e.g. rodents, zebrafish, chickens).

Note that this means that some "boundaries" in the literature are not "true boundaries" as we use the term here (e.g. Lee, 2017). The term "true boundaries" here most resembles the way that "boundaries" are typically used in learning theory literature. For example: "… boundary cues, such as a cliff face or the shape created by a walled enclosure, are distinct from landmarks as they tend to confine movement within a particular space" (Buckley, Smith & Haselgrove, 2014, p. 1184).

1.1. True Boundaries versus Visual Covariates

Looking at Table 1, one can view our main question as asking which distinctions matter: the top versus bottom only (visual covariates), or the left versus right only (true boundary status), or both, or neither. At stake is the interpretation of a long history of experiments that have frequently compared boundary exemplars to non-boundary exemplars (which crosses both distinctions), finding differences in reorientation (Cheng, Huttenlocher, & Newcombe, 2013; Lee, 2017), biases (Kosslyn, Pick, & Fariello, 1974; Sturz & Bodily, 2016), brain areas used for processing the stimuli (Doeller, King, & Burgess, 2008; Ito et al., 2015; Julian, Ryan, Hamilton, & Epstein, 2016), the specific algorithms for learning (Doeller & Burgess, 2008), neural alignment after disorientation (Keinath, Julian, Epstein, & Muzzio, 2017), and so on. These differences not only apply to adult humans, but to young children (Cheng et al., 2013; Lee, 2017), chickens (Lee, Spelke, & Vallortigara, 2012), zebrafish (Lee, Ferrari, Vallortigara, & Sovrano, 2015), and rodents (Cheng, 1986) as well. What are the key distinctions among the different items that these studies presented? What evidence do we already have to rely on that does not compare boundary exemplars to non-boundary exemplars, crossing both distinctions, but instead isolates just one distinction?

To answer this, we need to systematically examine comparisons across categories in the same half of Table 1 (i.e. keeping one factor constant but varying the other). There is already strong evidence in the left half of Table 1, comparing boundary exemplars to mere boundaries, finding a strong visual covariates effect. Presenting typical opaque walls (boundary exemplars) versus acrylic glass walls of the same size and shape (mere boundaries) to participants can bias memory of where the different items were in different ways (Kosslyn et al., 1974; Newcombe & Liben, 1982). Specifically, adult participants judged items within the same opaque walls as systematically closer to each other than they really were. They also judged items crossing opaque walls as systematically further apart. The same pattern was not seen for the acrylic walls. Earlier in development, young children

can successfully reorient to opaque walls but not acrylic walls (Gianni, De Zorzi, & Lee, 2018), suggesting that this distinction is important across the lifespan.

These studies (Gianni et al., 2018; Kosslyn et al., 1974; Newcombe & Liben, 1982) are examples of a precise isolation of one distinction, since they compare items with the exact same ability to impede navigation, but the items vary in how they look. Unfortunately, they are the last of such studies in the literature, and we obviously have more distinctions to examine. Instead now we have to rely on comparisons without a precise isolation. One study presented 2 cm tall rectangular solids along the ground (like very short walls) and a smooth hump created by a small pipe under a rug, versus a regular torso-height wall and a flat mat (Lee & Spelke, 2011). While these all look different and impede movement in slightly different ways, we would still generally say that the rectangular solid is a visual barrier (very easy to step over, so not a true boundary, but has important covariates like an extended 3D surface) and the same with the rug hump. In contrast, the mat is a non-boundary exemplar and the torso-height wall is a boundary exemplar. Given this interpretation, we can continue with comparisons.

Within the right half of Table 1, children reoriented to the visual barriers (2cm rectangular solid, rug hump) but not the non-boundary exemplar (flat mat), again suggesting a visual covariates effect like in the left half. Across the top half of table 1, children reoriented to the boundary exemplar (torso-height walls) and the visual barriers (2cm rectangular solid, rug hump) alike, speaking against a true boundaries effect. Unfortunately, we do not have any similar way to make a comparison on the bottom half. In summary, these studies are consistent with a visual covariates effect (effects in left half and right half) but not a true boundary status effect (no effects in top half, no studies in bottom half).

But this is not to say that a consensus view exists in favour of a visual covariates effect and against a true boundary status effect. Just last year, the following passage was printed in *Current Biology*:

> From insects to humans, animals construct metric spatial and temporal maps of their experienced environments. These spatio-temporal maps serve as the foundation for their behavior. A metric spatial map represents the shape of the navigable environment — the distances and directions between the surfaces and/or drop-offs that bound it. This remembered geometry provides a frame of reference within which location and direction vectors are defined. In its absence, an animal has no sense of where it is nor which way is which. (Gallistel, 2017, p. R108)

This asserts a dramatic cognitive effect (categorically disabling all spatial cognition) that is due to the function of the items in the environment (what is "navigable") – under our definitions here, it depends on true boundary status. That article might also be taken to implicitly deny the effects of visual covariates by the fact that it never mentions them.

In a few high-profile cases, this goes further and articles explicitly deny the effects of visual covariates on spatial coding. One pair of sister papers looked at learning mechanisms and brain regions when presenting boundary exemplars (large gray walls) versus non-boundary exemplars (various small items such as traffic cones). They conclude a strong categorical effect, specifically that true boundaries follow an incidental learning rule in the hippocampus and that non-boundaries follow an error correction rule in striatal areas (Doeller & Burgess, 2008; Doeller et al., 2008). They argue that these effects are not due to visual covariates on the basis of further manipulations that also compare boundary exemplars to non-boundary exemplars, such as a similar effect when the non-boundary exemplars are tripled in height. This is not as ideal as a comparison between a boundary exemplar versus a

visual barrier, or a mere boundary versus a non-boundary exemplar (i.e. isolating boundary status and keeping visual covariates constant).

There have already been a number of direct replies arguing against these conclusions (Austen & McGregor, 2014; Buckley, Smith, & Haselgrove, 2015; Kosaki, Austen, & McGregor, 2013; Mou & Zhou, 2013; Pearce, 2009). These replies show that the above effects can be reversed, for example, by adding more non-boundary exemplars (Mou & Zhou, 2013) or using a more salient corner of the boundary exemplars (Kosaki et al., 2013). As a whole this becomes difficult to interpret; the manipulations matter sometimes but not always, and not always in the same direction, so it is not obvious what drives effects.

The major gap that exists, which we fill here, is the need for more of the precise isolations across a single half of Table 1. In other words, we need truly definitive tests for the presence of a pure true boundaries effect and a pure visual covariates effect – ones with absolute precision in the way they control against effects of the other. For the true boundaries effect, this requires a comparison between a boundary exemplar and a visual barrier (different true boundary status) with absolutely no visual differences between the conditions whatsoever. For the visual covariates effect, this requires a comparison between a visual barrier and a non-boundary exemplar (different visual covariates) with absolutely no differences in the navigation-impeding functionality of the items whatsoever. With modern technology and modern Bayesian methods of analysis, we provide exactly those tests here.

1.2. The Present Study

Participants attempted to recall the locations of targets in immersive virtual environments surrounded on three sides by different items, varying across conditions. In the *plywood* condition, a set of walls were visually displayed in a way that they exactly coincided with an actual piece of plywood and gave participants the experience of being unable to move through them. In the *pass through* condition, the walls were instead presented in a space that

was actually empty and gave participants the experience of pushing their hand through them without resistance. In the *pass over* condition, the walls were below a translucent floor and participants experienced walking freely over them. This means that the *pass through* and *pass over* conditions were not true boundaries (obstacles to navigation) but that the items involved were visually identical to the *plywood* condition. To examine the other side of the question (i.e. to keep true boundary status constant and change the visual covariates), the *cones* condition replaced the walls with a set of traffic cones placed where the centers of the walls were. These virtual cones also could be passed through without resistance. The last remaining cell of Table 1, the mere boundaries, was omitted since it would have presented a great deal more practical (and perhaps even ethical) concerns with how to allow participants to safely experience invisible walls. These comparisons allow us a systematic examination of precise isolations of both effects, filling major gaps on the top half and right half of Table 1.

Given that boundary exemplars have been shown to create strong biases (Kosslyn et al., 1974; Newcombe & Liben, 1982), we formed our hypotheses in terms of bias and precision rather than just using overall error. If true boundaries are an important distinction, there should be higher precision and/or weaker biases with the *plywood* condition than the others, since it contains the only true boundaries. For brevity, we will call this a *boundaries per se hypothesis*. If visual covariates are an important distinction, there should be lower precision and/or stronger biases in the *cones* condition, since it uses items that are not visually like a typical boundary. For brevity, we will call this a *visual hypothesis*. Our specific approach and measure are most similar to those used in most developmental studies in this area (e.g. Lee & Spelke, 2011); it is typical to first confirm that there are no significant biases, then proceed to analyse accuracy (which is equal to precision with zero bias). Since we were both interested in when effects exist and when they do not, our main analysis uses modern Bayesian methods that can find evidence for either.

It is also important to consider that there may be a distinction between navigation, when an organism actually moves to a previously-experienced location, versus spatial memory, where they simply identify a previously-experienced location. The availability of movement can have an impact on spatial cognition (Lessels & Ruddle, 2005; Ruddle & Lessels, 2006); it is possible that boundaries would make a difference when navigating even if they made no difference to spatial memory when standing in one place, especially since the act of navigation could make an obstacle to navigation more relevant. To investigate this possibility, we recorded both no-movement (memory only, i.e. pointing) and movement (navigation, i.e. walking) responses, and then looked for an interaction between experiment condition (the nature of the items present) and response modality (walking to a target versus pointing to it), in addition to main effects of condition.

2. Method

2.1. Summary

Participants were given a spatial memory and navigation task in one of four immersive virtual reality environments (Figures 1 and 2). Within an approximately $4m^2$ area with different surrounding visual (and tactile) features, they were shown three small ‘spaceships’ and then ‘teleported’ to a new viewpoint within the arena and asked to either point to the spaceships (spatial memory) or walk over to their locations (navigation) in order.

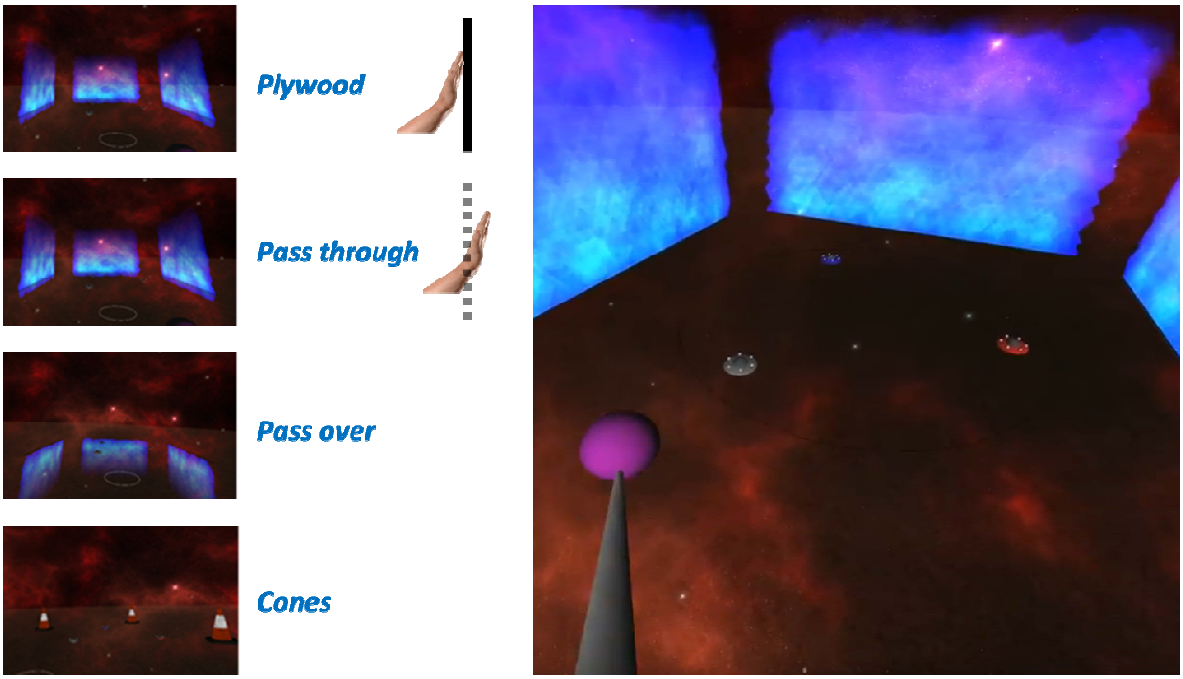

Figure 1. The experiment immersed participants in one of four different environments across conditions. In terms of appearance, the environments for the *plywood* and *pass through* conditions were visually identical in every detail. The *pass over* condition only looked different in that the walls were under the floor, but the walls themselves joined the floor at the same place and otherwise looked identical. The *cones* condition replaced the walls with traffic cones. In terms of how items functioned, only the walls in the *plywood* condition gave any resistance when participants attempted to pass through them. These conditions allow us to dissociate how an items true boundary status affects spatial memory (*plywood* versus *pass through/over*) and how an item's visual appearance affects spatial memory (*cones* versus *pass through/over*).

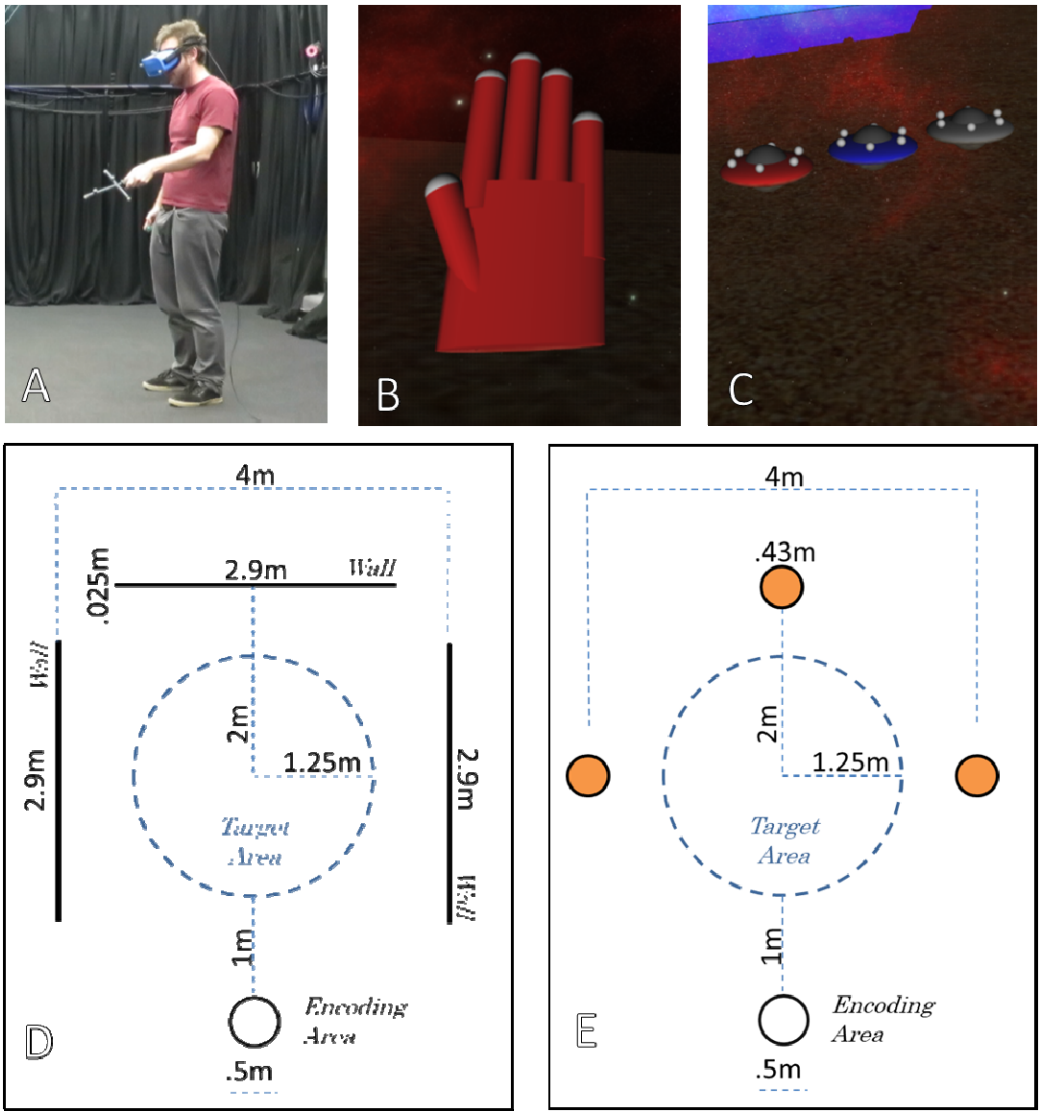

Figure 2. Here we give additional information about the methods. (A) A photograph of a person participating in the experiment. (B) The red 'robot hand' that moved with the right hand of participants in the virtual world. Before data collection, participants used this to experience what items they could/could not move through. (C) The targets, in a line here to see easily – though they were placed randomly in the experiment and thus rarely appeared in a straight line. (D) A diagram of the *plywood*, *pass through*, and *pass over* conditions. (E) A diagram of the *cones* condition. In short, participants were asked to stand in the Encoding Area and watch the three targets appear and disappear in order. They were then 'teleported' (screen faded to black, 'camera' moved, screen came back up) to a point on the edge of the target area. They then indicated where they remembered the three targets in order.

2.2 Participants

Eighty undergraduates were recruited to participate. They were given either a credit hour towards a program where students volunteer in each other's studies or £8. The study was

approved by the local Ethics committee and participants gave informed consent. Participants were excluded if they had abnormal vision and could not wear contact lenses. Twenty participants each were randomly assigned to the conditions (see below): *plywood* (10 female, mean age = 23.45 years); *pass through* (10 female, mean age = 22.30 years); *pass over* (10 female, mean age = 26.2 years); and *cones* (10 female, mean age = 21.50 years). This sample size was chosen mainly because it is slightly larger than the number of participants in developmental studies that have found related effects (e.g. Lee & Spelke, 2011). The design also has the added advantage of a much higher number of trials per participant (48 here versus 4 in that case).

2.3. Apparatus

Participants wore an Oculus Rift headset (Consumer Version; Menlo Park, CA, USA). The headset was tracked continuously by the small reflective markers feeding into a Vicon Bonita motion tracking system (Oxford, UK). They were also given a motion-tracked 'wand' for indicating responses, made of some PVC and a screwdriver handle (see Figure 2A), plus a small motion-tracked glove on their right hand. The virtual environment was programmed in WorldViz Vizard 5. With real-time updating of the participant's and headset's position from the motion capture markers, participants were able to freely traverse a space of about 5m x 10m, with approximately 4m x 4m used during this study.

2.3.1. Virtual environment.

The virtual environment for the *plywood*, *pass over*, and *pass through* conditions featured three blue walls set at right angles (see Figure 1). They were adapted from a fire effect in WorldViz Vizard 5. They were formed of a continuous set of translucent hexagons that moved slowly and drifted randomly. This was done so that the participants would not necessarily have a strong expectation about its status as a boundary or non-boundary. To enable the *plywood* condition, the virtual wall to their left was rendered in the same place as a

real 4ft x 8ft (approx. 1.2m x 2.4m) piece of plywood which participants could touch. It was mounted up on the wall so that the top edge was above their eye level. To enable the *pass through* condition, the virtual wall to their right corresponded to an empty space in the lab which participants could put their hand through without any resistance. For the *pass over* condition, the walls appeared below the translucent floor but could still clearly be seen. Under the boundaries per se hypothesis, the *plywood* condition should show higher memory precision and/or weaker biases than the other three conditions.

In the *cones* condition, there were instead three traffic cones (dimensions conforming to motorway regulation in the UK) placed where the centers of the walls items were in the other conditions. The cones were 67.5 cm in height, 43 cm across the base, and colored orange and white (see Figure 1). Under the visual hypothesis, this condition should differ from the other three in terms of bias and/or precision.

There was also a skybox rendered at an infinite distance with the appearance of outer space nebulae (i.e. a redundant method for participants to reorient themselves, but without providing distance information). The floor surface was made of a translucent sand texture (20% opacity). Participants also saw a virtual projection of their wand and of a red ‘robot hand’ where their right hand was (Figure 2B). The participants were asked to hold the wand in their left hand when they were not actively using it, but to use both hands to point as accurately as possible when indicating locations during the main task. The motion capture markers on the right hand were placed on the back side of the hand so that they did not interfere with this.

2.3.2. Stimuli

On each trial, the stimulus was a set of three target locations on the floor to remember. This was shown by having three small coloured spaceships (Figure 2C) appear and disappear in sequence at different positions. The ships were red, blue, and grey on their outer hulls, with a

grey center and six small white lights on their top sides. They appeared by first being shown as a flat disc and then stretching to their full vertical extent. Then they were removed by flattening again and then disappearing. Each was visible for 1s plus or minus the screen refresh time (1/90th of a second). Spaceship locations were randomly drawn from a uniform circular distribution with a radius of 1.25m around the center of the arena (Figure 1D-E, "Target Area"), constrained only in that they could not overlap each other.

2.4. Procedure

Participants were not allowed to view the actual lab before entering. They were fitted with the headset outside and then led in. Each of the three conditions had a pre-testing procedure that drew their attention to the items in the environment at the start of each block. For the *plywood* condition, they walked over and touched the plywood that was tracked onto a virtual wall. For the *pass through* condition, they walked over to a virtual wall projected into empty space and were instructed to try putting their hand through it. For the *pass over* condition, they were instructed to walk over the same virtual wall and see what the wall looked like. For the *cones* condition, they were asked to go push the wand through each of the cones.

There were a total of four blocks of twelve trials. At the beginning of each trial, participants stood inside a small white circle, the same on every trial (Figure 2D-E, "Encoding Area"), and viewed the stimulus. Participants were then 'teleported' – the screen faded to black, the virtual camera moved, and then faded up from black – to a place around a 2.5m radius circle in the middle of the three walls (Fig. 2D-E, "Target Area"). The white circle was no longer visible. Their view also rotated. The rotation amounts were random but within the constraint that each block had six rotations under 90 degrees and six rotations above 90 degrees (180 being the max possible), three to the left and three to the right. Participants were assigned randomly to indicate their responses by either pointing with the wand or by walking for the first block, and then the blocks alternated (so if they pointed in

block 1, they also pointed in block 3). A small inverted cone was rendered on the floor to make it as clear as possible where each pointing or walking response would be recorded. In the pointing case, the cone marked the point where a straight line from the wand intersects the floor, while in the walking case, it was slightly in front of them – specifically, it was 25cm in front of the center of their head in the direction they were facing. The cone's colour was matched to the spaceship. This was repeated for all three spaceships, with the coloured cones remaining visible from previous responses. The responses were collected as quickly as participants made them (no additional delay was imposed by the experimenters). The spaceships then re-appeared and the participants were allowed to see what errors they made. They then returned to the encoding area for the next trial. Breaks were given between blocks as needed. Testing typically took 45 minutes to an hour.

This procedure essentially results in 48 trials each yielding fourteen figures: the x-axis placement and z-axis placement of each target and each response, plus the rotation amount and the block number. This gave us a rich basis for assessing both the bias and precision for each participant. This should allow us to detect any differences in the spatial coding that the different conditions caused on average.

3. Results

Overall, results suggest an average difference in how participants coded the locations in the *cones* condition versus the other three (supporting an effect of visual covariates) but not a difference between the *plywood* condition and the other two conditions with walls (pointing away from an effect of boundary status). This appears to be driven foremost by differences in biases, although a lower estimated memory precision in the *cones* condition also contributes.

3.1. Descriptive Statistics

We ultimately wanted to use a modern Bayesian method to look both for evidence that some conditions differed and that some were not different. This requires an explicit model of the task. To guide development of the model, we first looked at descriptive statistics. The most basic of these is presented down the right column of Figure 3, where the radius of each circle represents the median distance between target and response for targets in that quadrant for that condition. This gives a sense of total error that our model must explain, highlighting that it is actually a fairly large amount for an adult. The left column shows the average bias for different segments of the target space as a function of condition. Comparing the size of these arrows with the radius of the circles down the right column shows that bias is a major portion of total error. It is also important that the arrows within each condition appear to converge in a single location. It can further be seen informally that the arrows converge in a different place for the *cones* condition than the other three, which we can verify formally later.

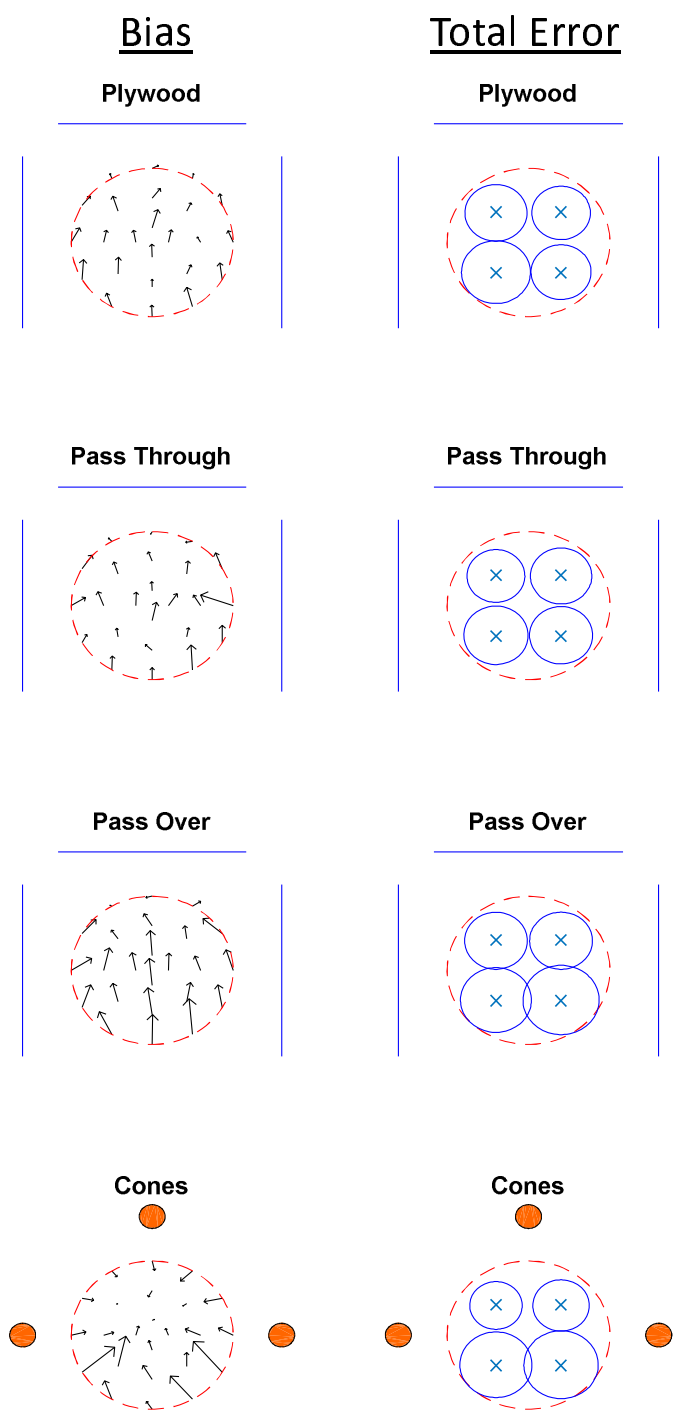

Figure 3. Down the left column, the mean of signed error is shown as a function of condition and placement of the target. Down the right column, the radius of each circle shows the median distance between target and response for targets in that quadrant of that condition. These respectively give a sense of bias and total error.

The simplest way to parse away the bias and get a rough sense of precision is with Spearman's Rho (Figure 4). This lets us get a sense of how well a given target predicts a given response even if the relation between the target and mean response is highly non-linear, as we would expect from the arrows in Figure 3. For simplicity, as formal measures of differences were examined later with the model, we pooled all available data from all subjects and trials together along both axes. The overall rho-value between target and response is 0.80, suggesting first that the task was not too difficult for the participants. Breaking this down by condition, we see the *cones* falling slightly lower and see the other three remaining relatively consistent. Looking by rotation, we see the expected trend where further rotation (i.e. a larger change between encoding and retrieval) leads to less precision. By block, we see a moderate learning effect, with higher precision in later blocks. There is also a very small effect where responses were more precise when walking than pointing.

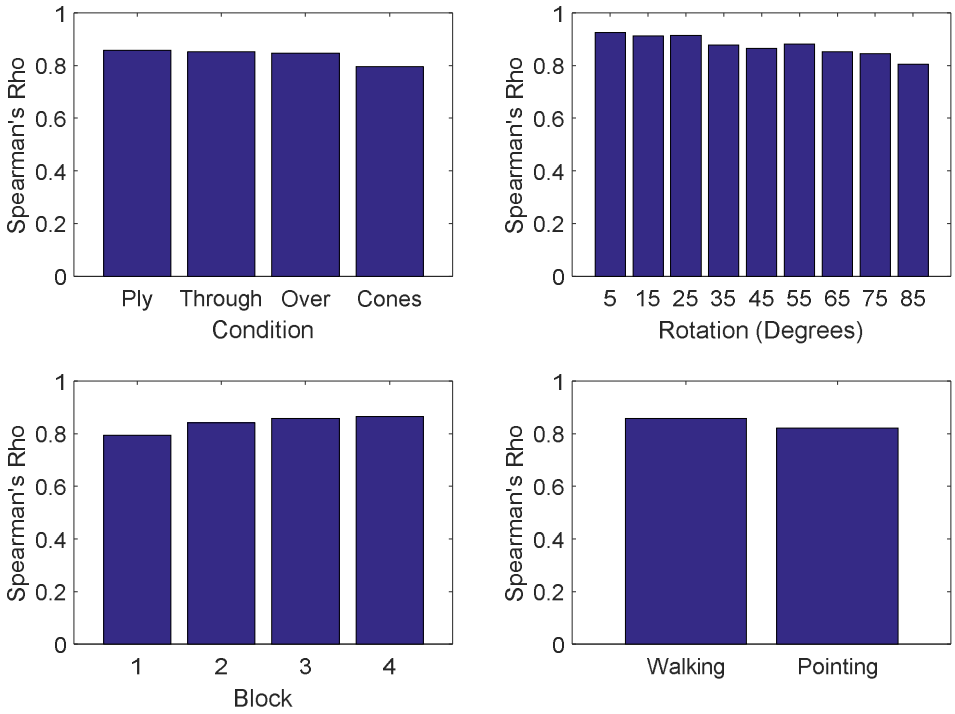

Figure 4. Precision in responses as a function of condition (top left), rotation of the participant between encoding and response (top right), block number (bottom left), and response modality (bottom right). Values were calculated by pooling across all participants

and both axes. Error bars are omitted since the posterior distributions presented later give a more realistic sense of measurement error.

Based on Figure 3, we modelled these data in a way where each person has a specific point that their responses are biased towards by a certain strength, corrupted by random memory noise. Based on Figure 4, the model also features a term for the rotation amount and the block number to influence precision. We can then use Deviance Information Criterion (Spiegelhalter, Best, Carlin, & van der Linde, 2002) to assess how different nominal groupings of the different conditions affects the predictive value of the model (i.e. to test for/against differences between conditions). For example, DIC should improve when we collapse the *pass over* and *pass through* conditions if their relevant parameters are actually quite similar, since it means that more data can be used to predict future participants in either condition. In contrast, DIC should worsen if they are actually dissimilar, since it would then be more accurate to just use each condition's separate data to predict future participants.

3.2. Model Analyses

The description of our formal model-based analysis proceeds in three stages. First, we describe the model (a typical model of Bayesian reasoning with a prior and likelihood using bivariate normal distributions and additive precision) in a way that is designed to help the reader gain an intuition of how it functions. Full formal details are provided in Appendix A. Second, we state the main result. Third, we look at the posterior distributions of the model to see what is driving the main result.

3.2.1. Model description

After a target is shown (Figure 5, left panel) and removed, its memory trace degrades during the 'teleportation'. By the time recall is occurring, the memory trace (Figure 5, middle panel) is a draw from a bivariate Gaussian with the target as the mean. In addition to the trace, there is a prior distribution that the participant is using. With their relative precisions used as

weights, the prior's center and the memory trace are averaged to determine the response (Figure 5, right panel).

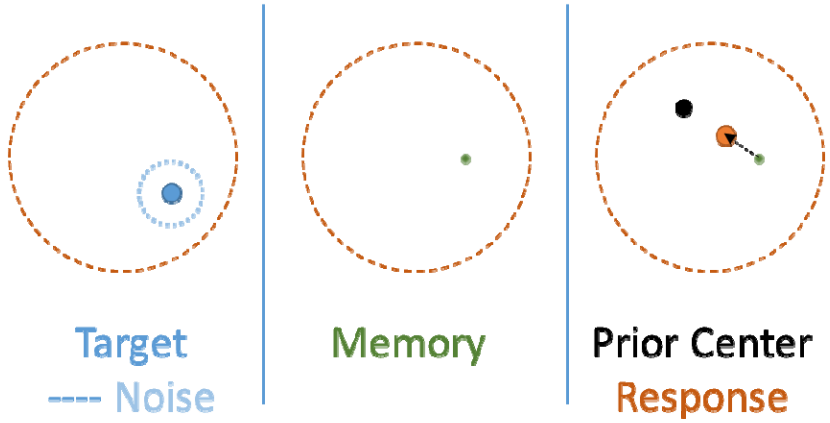

Figure 5. An example trial of how the model works. The memory trace of the target in the left panel degrades over the 'teleport' to the place in the middle panel. The participant then takes a weighted average of their memory (green dot) and their subjective prior (black dot) to determine the response (orange dot) in the right panel.

This model therefore has four parameters per participant: the prior's center on the x-axis (*Prior X*), the prior's center on the z-axis ("forwards" for the participant standing in the encoding circle; *Prior Z*), the precision of the memory traces (*Memory Tau*), and the precision of the prior distribution (*Prior Tau*). The bias they show is determined by the prior's center (where they show a bias towards) and by the prior precision (how strong that bias is). Their memory precision is generally the precision of interest, controlled directly by Memory Tau, but the overall precision of their responses is additively determined by the memory precision and the prior precision.

It is worth noting that the mathematical mechanics involved in this model can be re-framed equally as a bias existing towards a certain point with a certain strength, trading off against their memory and their confidence in that memory. It could also possibly be framed as over- or under-representation of equal portions of the space. We do not have the data to verify the extensive predictions that come along with assuming fully optimal Bayesian reasoning.

The rest of the model then assumes that individuals, with their four individual-level parameters, are drawn from a condition-level distribution with two parameters per individual-level parameter: one for the mean value within the condition (Prior X Mean, Prior Z Mean, Memory Tau Mean, Prior Tau Mean), and another for the spread (Prior X Tau, Prior Z Tau) or the shape/spread of the Gamma distribution that they are drawn from (Memory Tau Alpha, and Prior Tau Alpha). The posterior fitting process flows in both directions, with the condition-level distributions responding to individual-level parameters and vice versa.

We also created a version to look for interaction effects. In this version, each participant has a separate Prior X and Prior Z parameter for walking and pointing, but they are correlated in a bivariate normal. The Memory Tau and Prior Tau parameters are replaced by their logarithms, which are given the same treatment: separate but correlated across modalities.

3.2.2. Main result

The main result is that the Deviance Information Criterion (DIC; see Table 2) is best when grouping the conditions with walls together into one nominal condition with the same group-level parameters and keeping the *cones* condition separate, while also keeping the pointing and walking trials together within conditions (second row to the bottom, highlighted). This is the best DIC by a margin of 30 (49 below baseline model, whereas the next best is 19 below). For calibration, imagine two models with the same number of effective parameters. If one fits the data 150 times worse on average, that one will have a mean deviance and thus DIC that is higher by 10. DIC also has an explicit penalty for model complexity in units of deviance. The selected model has the lowest (best) DIC for a combination of both reasons, having the best average fit (by 11) and the second-smallest complexity penalty (smallest was the model with no effect of condition whatsoever).

Table 2. DIC Results.

Condition Groupings	Interpretation	Mean Deviance	p_v	DIC
1 = Plywood, 2 = Pass Through, 3 = Pass Over, 4 = Cones	(Full Effects Baseline) Every condition difference matters	28,051	427	28,478 (+/-0)
1 = {Plywood, Pass Through, Pass Over, Cones}	(Null Effects) No condition difference matters	28,133	391	28,523 (+45)
1 = Plywood, 2 = {Pass Through, Pass Over}, 3 = Cones	Both boundary status and visual covariates matter	28,052	422	28,474 (-4)
1 = Plywood, 2 = {Pass Through, Pass Over, Cones}	Boundary status matters, but not visual covariates	28,044	415	28,459 (-19)
1 = {Plywood, Pass Through, Pass Over} 2 = Cones	Visual covariates matter, but not boundary status	28,033	396	28,429 (-49)
1 = {Plywood, Pass Through, Pass Over, Cones} but with separate correlated parameters for walking and pointing	Separation of parameters by response modality (potential interaction effects)*	32,189	3,147,591	3,179,779 ($+3x10^6$)

*Note: for brevity, other groupings are omitted for the interaction effects, but they were all worse by margins are that functionally infinite (mean deviance up by >6,000, total DIC up by millions).

This favors an interpretation that visual covariates matter, but not true boundary status. More formally, it suggests that the best way to predict future data is to use all the recorded participants from the *plywood*, *pass over* and *pass through* conditions together to predict the performance of a new participant in any of those three conditions, but to only use the recorded *cones* data to predict the performance of a new participant in the *cones* condition. Note that this is the version where walking and pointing are kept together; all models that separated these suffered an enormous complexity penalty for nearly doubling the number of nominal parameters, but did not gain anything notable in terms of mean deviance.

3.2.3. Posterior distributions

What is driving the differences in DIC? An examination of the posterior distributions (Figure 6, *cones* in purple) using the full effects baseline model shows three places where the *cones*

condition diverges from the rest to a notable degree: the average center of the inferred prior on the z axis is lower for the *cones* condition than the other conditions, the mean precision of the inferred prior is higher, and the mean precision of their memory is lower. In other words, on average, the biases they showed were pulled towards a different place (nearer the encoding point), and pulled there stronger, plus they had lower precision (more noise) in their memory of locations in the task.

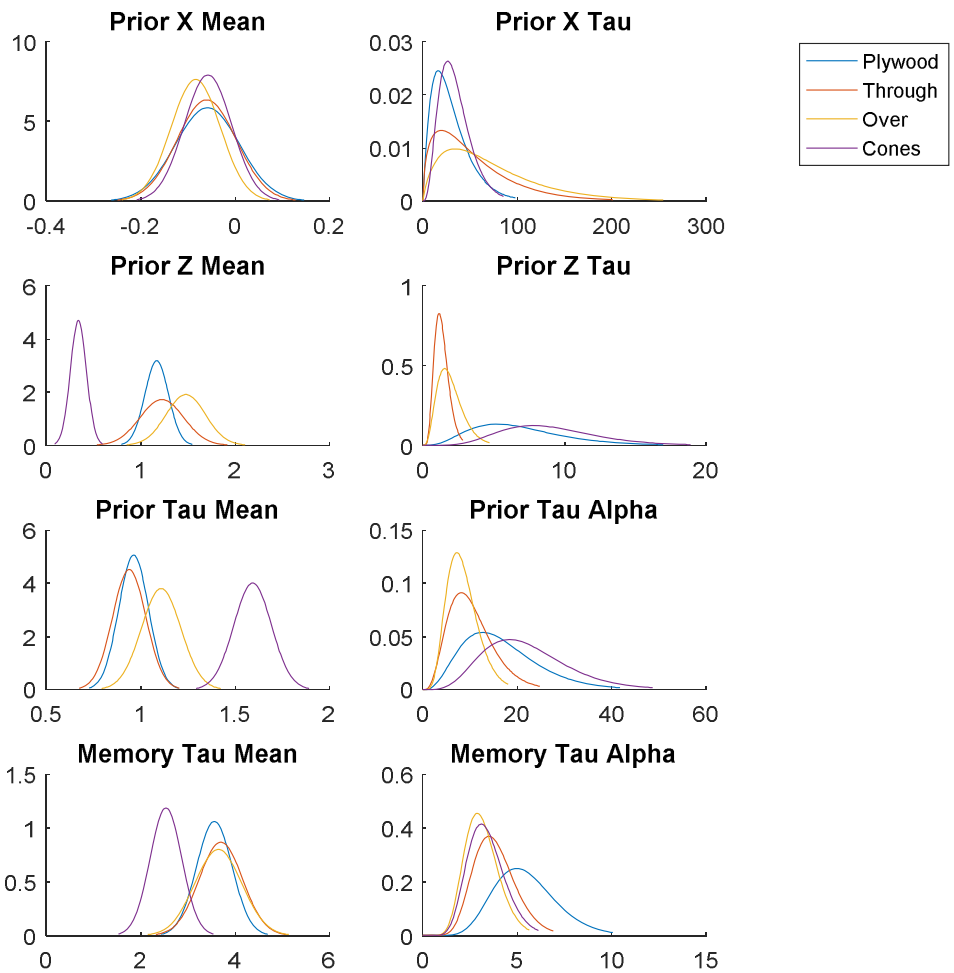

Figure 6. Posterior distributions for the four different conditions over the eight condition-level parameters. The differences in the *cones* (purple) condition explain how that condition differed and why DIC was lowest when grouping the others together. All units are in meters.

To make the bias difference easier to visualize, we also plot a 95% credible region around the mean prior point for each condition in Figure 7. Compare with the descriptive Figure 3 above to see that these fits are sensible. This is interesting because the *cones* fit is

both quantitatively and qualitatively different. Since it is near the center of the actual area where the targets appear, it might reflect a default strategy of pointing near the center to minimize error when memory is not trustworthy.

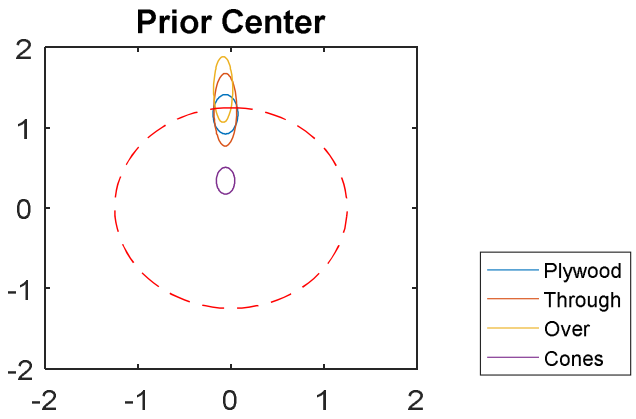

Figure 6. Visualization of the different prior centers on average over participants in each condition. Each ellipse represents a 95% credible region.

In contrast to the *cones*, the *plywood* condition is not clearly separated from the other two conditions with walls on any condition-level parameter. It is perhaps closest to showing a difference with the *pass through* and *pass over* conditions in terms of the Prior Z Tau parameter, which is somewhat awkward to interpret even if we ignore the overall DIC results; it would mean that participants in that condition were more consistent in where they placed the center of the prior on the z axis (but not the x axis, and arriving at the same mean placement).

For completeness, we also report that the mean posterior Rotation Beta was -.006 (95% Credible Interval: -.0064 to -.0056), suggesting that a trial where participants were rotated to the far side had 2.94 times the precision (about 58% of the standard deviation) of trials where they did not rotate at all. The effects of the blocks, in order, were 0 (fixed), 0.22 (0.16 to 0.28), 0.40 (0.34 to 0.46), and 0.38 (0.33 to 0.44). For reference, a value of 0.40 translates to 49% more precision (82% of the standard deviation).

4. Discussion

The model comparison method considered different models where visual covariates affect spatial coding, true boundaries (obstacles to navigation) affect spatial coding, both, or neither. There were also versions where these effects interacted with response modality (walking vs. pointing). The preferred model, by a wide margin (30 DIC), is one where visual covariates affect spatial coding but not true boundaries (also not interacting with response modality). In other words, in the first study to fully dissociate true boundary status and visual appearance, we have found positive reasons to both believe that visual covariates do matter for spatial coding and that true boundary status (specifically meaning an obstacle to navigation) does not have the same effect. Much of the difference in coding was driven by the bias shifting inside the space, but the posterior fits also point towards a lower memory precision in the presence of the traffic cones versus the walls.

These results are perhaps easiest to accommodate under a theory that focuses on the presence of extended 3D surfaces (Lee, 2017; Lee & Spelke, 2011), a visual covariate, rather than true boundaries (obstacles to navigation). Under this theory, all three conditions with walls visually presented an extended 3D surface, so it is expected that spatial coding would be the same; the cones lack such a surface, so it is expected that coding would differ from the other conditions. More broadly, it remains plausible that boundary *perception* has special effects even if boundaries *per se* do not. It is possible that people perceived all of the walls to be boundaries even despite repeated motor-haptic experience that the *pass over* and *pass through* conditions are not. This perception could then control coding. This might be akin to a visual capture phenomenon (Hay, Pick, & Ikeda, 1965; Pavani, Spence, & Driver, 2000).

To pursue that line of theory development further, it would be crucial to have a way of objectively measuring boundary perception. If we state that the perception of boundaries has certain effects on spatial cognition, then classify items as being perceived as boundaries or not on the basis of those effects, we make a circular argument. Avoiding the circularity

would require something like a measurement of avoidance behaviour in a navigation task or perhaps a set of neural signatures that are selectively attentive to the blocking of navigation.

The differences in memory precision of estimates are also quite easily accommodated by theories that put forward a general adaptive mechanism for navigation and spatial memory, either explicitly endorsing the application of classic learning theory models (Pearce, 2009) or suggesting that the most useful method is employed in a Bayes-optimal fashion (Xu, Regier, & Newcombe, 2017). Under these kinds of theories, all conditions with wall-like surfaces would provide the same basic way of remembering where things were (by referencing the distances and directions to the places where the items met the floor) and they would all provide the same error signals when responses were inaccurate; they would all be equally useful if used according to domain-general principles, so it is also expected that performance would be the same. In contrast, the cones are less useful because they don't provide the same breadth of reference points (Mou & Zhou, 2013), so precision there is lower. Explaining how or why the bias was different is not as clear, but not necessarily a violation of these theories either. Where these theories have difficulty is in explaining other data, such as why a flat mat on the ground with the same edge as the walls does not facilitate orientation for young children (Lee & Spelke, 2011).

Extending the Bayesian aspect of this interpretation could plausibly be a fruitful way forward for understanding this kind of task. As it stands, it is not clear why a model that relies on Bayesian inference would have different priors in the *cones* condition versus the ones with walls, but there is also no particular reason why it shouldn't. An independent study of the priors that participants bring to different environments could work towards a theory to explain this and predict the priors in future experiments. As noted in the model description, it is also possible that some very similar effect is being captured instead; results look like what we would expect if some areas of the space were over-represented in memory and some were

under-represented, for example. It would also be interesting to see if the biases are present in perception, memory, response, or some combination thereof.

These results are much more difficult to accommodate under a theory that places special focus on a second, highly-specialized, low-error module that attends only to true boundaries (obstacles to navigation) (Doeller & Burgess, 2008; Gallistel, 2017). Under this kind of theory, we would expect that the true boundaries would be selectively involved in the formation of a 'cognitive map' in the hippocampus (Doeller et al., 2008), which should have some measurable effect on how locations are encoded (increasing precision or reducing bias) (see Gallistel, 2017 for an argument to this effect when supporting the boundaries per se hypothesis). Instead, it fits the current data better to posit that both true boundaries and non-boundaries alike have access to this system when they are visually identical.

The use of immersive virtual reality can be a cause for concern in some situations but not the present study. The fidelity of immersive virtual reality simulations for studying spatial cognition has undergone extensive examination, far more than most Psychology methods, often uncovering systematic linear underestimation of egocentric distances (Renner, Velichkovsky, & Helmert, 2013). However, this effect is generally attenuated greatly, if not eliminated, by a "walking intervention" (i.e. short experience moving through the space via walking), which our participants had, and is generally much less necessary for modern head-mounted displays like ours in the first place (Kelly, Cherep, & Siegel, 2017). Several complex spatial effects have been shown to be the same in immersive VR and real stimuli (Kelly, Avraamides, & Loomis, 2007; Kelly & McNamara, 2008; Negen, Heywood-Everett, Roome, & Nardini, 2018; Negen & Nardini, 2015; Williams, Narasimham, Westerman, Rieser, & Bodenheimer, 2007). In terms of boundaries specifically in immersive VR, participants go to great effort to avoid striking things that look like real boundaries even when they know they aren't really there (Fink, Foo, & Warren, 2007), with their paths in

novel VR environments being very closely predicted ($R^2 > .95$) by parameters gathered in dissimilar real environments. More troubling issues may be present when using desktop VR instead of immersive VR, yet even that approach captures individual differences that are also seen in the same participants with real environments (Richardson, Montello, & Hegarty, 1999). Perhaps even more to the point for the present study, the crucial difference between the *plywood* vs. the *pass through* and *pass over* conditions was not delivered through VR at all – it was a real tactile difference between the subject's real hand touching a piece of real plywood or not.

4.1. Which Visual Covariate?

Up to this point, we have only interpreted results in terms of true boundaries versus visual covariates. Now that we have made a conclusion on that front, a natural question is to ask which visual covariates are important. Here we have to be more tentative, but we can point out that a view focusing on extended 3D surfaces (Lee, 2017) fits the data we have observed. This would especially explain why we did not measure differences between the *pass over* and *pass through* conditions. It also correctly predicts that children would reorient to extremely short 'walls' but not flat mats on the ground or columns (Lee & Spelke, 2011). An alternative, but highly related, way of approaching this is to focus on the density of distinctive local points on the different items in the space (Mou & Zhou, 2013). This leads naturally to the prediction that the *plywood*, *pass over*, and *pass through* conditions would be similar and the *cones* would differ; the walls have two distinctive ends that are further apart than any two points on the traffic cones, meaning that points in the encoding space are closer on average to a salient local point. It is less clear why children would not reorient to flat mats on the ground in this view.

A large-scale study of parametric variation of several different item parameters might be an invaluable resource in answering some of these questions. For example, there might be

a strong discontinuity in the effects due to horizontal extent as an item crosses over from being a ‘column’ to being a ‘wall’, or it could be a smooth function.

4.2. Broader Definitions of “Boundary”

Throughout the above text, we used a narrow definition of “true boundary” where we just focus on its function as an obstacle to movement, in line with the definition of “boundary” found in learning theory texts (Buckley et al., 2015). In the literature there are also broader definitions. Under one such definition (Lee, 2017), which defines a boundary as an object with an extended 3D visual surface, we would describe the results differently. In that case, boundaries have two aspects: their physical function and their visual appearance. The present results place emphasis on the role of the visual appearance over the function, as the visual aspect controls the bias and precision of spatial coding in the environment.

In an even broader sense, the word “boundary” can have a metaphorical or social meaning. In that case, we would describe the present results as being relevant only to *physical* boundaries rather than *social* boundaries. However, for a future study, it would be possible to do something very similar and manipulate the social boundary status of items. It would be trivial to invent a cover story to encourage and praise one group of participants for crossing the walls in a pre-test task, then invent another story to discourage a different group from crossing them. Differences in spatial coding could then be assessed in a similar way.

5. Conclusion

Experiencing that an item is a true boundary (obstacle to navigation) or not, independent of visual covariates, does not directly affect adult participants’ coding of the locations around it. In contrast, non-boundaries that vary in visual appearance can lead to substantial differences in performance. This is the clearest evidence to date that the typical boundaries in natural scenes have their special effects on spatial cognition because of visual

covariates such as horizontal extent, the presence of extended 3D surfaces, or large-scale structure – not because they are true boundaries.

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Appendix A

This section gives a full formal description of the model that was applied to the data.

The model has 4 global parameters, 8 condition-level parameters per condition, and 4 individual-level parameters per participant.

- Rotation_Beta (global) controls how much rotating a participant (i.e. how far away the recall viewpoint was from the encoding viewpoint) affects the precision of their memory. It was given a prior of a normal distribution with mean 0 and precision 0.01.
- Block_Beta[2-4] (global) control how much a trial existing in blocks 2-4 affects the precision of memory. They were given priors of normal distributions with mean 0 and precision 0.01. A trial in block 1 has this set to 0, which does not affect precision, as a way of identifying the model.
- Prior_X_Mean (condition) is the center of the condition-level distribution of the priors' x-axis values. It was given a normal prior with mean 0 and precision 0.01.
- Prior_X_Tau (condition) is the precision of the condition-level distribution of the priors' x-axis values. It was given an exponential prior with rate of 0.01.
- Prior_Z_Mean and Prior_Z_Tau (condition) are the same as the X-axis parameters above, except on the Z axis.
- Memory_Tau_Alpha (condition) controls the shape of the gamma distribution from which individual memory precisions are drawn for participants in that condition. It was given an exponential prior with a rate of 0.01.
- Memory_Tau_Beta (condition) controls the rate of the gamma distribution from which individual memory precisions are drawn for participants in that condition. It also has a prior distribution of an exponential with rate of 0.01.
- Prior_Tau_Alpha and Prior_Tau_Beta (condition) are the same as just above but for the precision of the prior for that participant in that condition.

- Prior_X and Prior_Z (individual) together encode the center point of each participant's inferred prior. Prior_X is drawn from Normal(Prior_X_Mean, Prior_X_Tau $^{-1/2}$) and the same form for the Prior_Z.
- Memory_Tau and Prior_Tau (individual) together encode the precision of the participant's memory for a trial with 90 degree absolute rotation in block 1, and the precision of the inferred prior. Memory_tau is drawn from a gamma distribution with shape Memory_Tau_Alpha and rate Memory_Tau_Beta, and the same form for Prior_Tau.

For a given pair of target and response, we then assume that a response is drawn from a bivariate normal with calculated (non-stochastic) parameters for the means and standard deviation, assuming the covariances to be zero and the standard deviation to be the same in both axes.

The standard deviation is the total precision to the power of negative one half. The total precision has two additive components. The first is the prior precision. The second is the memory precision, which is Memory_Tau for that participant times exp(Rotation_Beta*abs(90-Rotation)) times exp(Block_Beta[Block]).

The mean is a weighted average between the target's location and the prior's center. The weight for the target's location is calculated by dividing the memory precision by the total precision. The weight for the prior's center is calculated by dividing the prior precision by the total precision. This is done in both axes.

This model purposefully makes several omissions that we can now explain. There is no explicit correlation between responses within the same trial. This was driven empirically, as Pearson's r values between the (response-target) values were relatively low within the same trial, between -0.05 and 0.25. We also saw that the model's assumption structure

provide certain kinds of similarity between responses on the same trial anyway, such as a common total precision, as they all share the same parameters.

The model also omits different effects of block or rotation by condition. This was done for two reasons. First, because we wanted to have a model where the response modalities were separated into different conditions. Having these effects vary by condition would then become much less stable, as participants only completed two block numbers in each response modality. Second, we did not have any a priori reason to think they would vary by condition.

The interaction model replaced Memory_Tau and Prior_Tau with the logarithms, then made each participant-level parameter subject to a bivariate normal distribution separated by response modality. The priors were a conjugate normal-wishart model: means of zero for the means, precisions of .01 for the means, zero correlation in the priors over means, and a wishart distribution with a rank of 2 and an identity matrix for omega.

Below is the precise WinBUGS Code used for the main model:

```
model{
for (i in 1:nConditions){
   CenterXMean[i] ~ dnorm(0,.01)
   CenterXTau[i] ~ dexp(.01)
   CenterZMean[i] ~ dnorm(0,.01)
   CenterZTau[i] ~ dexp(.01)
   TauAlpha[i] ~ dexp(.01)
   TauBeta[i] ~ dexp(.01)
   TauMean[i] <- TauAlpha[i] / TauBeta[i]
   PriorTauAlpha[i] ~ dexp(.01)
   PriorTauBeta[i] ~ dexp(.01)
   PriorTauMean[i] <- PriorTauAlpha[i] / PriorTauBeta[i]
}
TauBlockEffect1 <- 0
TauBlockEffect2 ~ dnorm(0,.01)
TauBlockEffect3 ~ dnorm(0,.01)
TauBlockEffect4 ~ dnorm(0,.01)
TauBlockEffect[1] <- TauBlockEffect1
TauBlockEffect[2] <- TauBlockEffect2
TauBlockEffect[3] <- TauBlockEffect3
TauBlockEffect[4] <- TauBlockEffect4
TauRotationEffect ~ dnorm(0,.01)
```

```
for (i in 1:80){
   CenterX[i] ~ dnorm(CenterXMean[ConditionByParticipant[i]],
         CenterXTau[ConditionByParticipant[i]])
   CenterZ[i] ~ dnorm(CenterZMean[ConditionByParticipant[i]],
         CenterZTau[ConditionByParticipant[i]])
   Tau[i] ~     dgamma(TauAlpha[ConditionByParticipant[i]],
         TauBeta[ConditionByParticipant[i]])
   PriorTau[i] ~
         dgamma(PriorTauAlpha[ConditionByParticipant[i]],PriorTauBeta[ConditionByP
         articipant[i]])
}

for (i in 1:N){
   TauTrialPerception[i] <- Tau[Participant[i]] * exp(TauBlockEffect[Block[i]]) *
         exp(TauRotationEffect * Rotation[i])
   Weight[i,1] <- TauTrialPerception[i]    / (TauTrialPerception[i] +
         PriorTau[Participant[i]])
   Weight[i,2] <- PriorTau[Participant[i]] / (TauTrialPerception[i] +
         PriorTau[Participant[i]])
   muX[i] <- Weight[i,1] * XTar[i] + Weight[i,2] * CenterX[Participant[i]]
   muZ[i] <- Weight[i,1] * ZTar[i] + Weight[i,2] * CenterZ[Participant[i]]
   TauTrial[i] <- TauTrialPerception[i]+PriorTau[Participant[i]]
   XRes[i] ~ dnorm(muX[i],TauTrial[i])
   ZRes[i] ~ dnorm(muZ[i],TauTrial[i])
}

}
```