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Cue integration and competition during navigation

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ABSTRACT

Navigation is influenced by body-based self-motion cues that are integrated over time in a process known as path integration, and also by environmental cues such as landmarks and room shape. This project explored whether humans combine path integration and room shape cues when returning to a previously visited location and connects human cue integration research to animal cue competition research. Participants walked an outbound path in an immersive virtual environment before attempting to return to the path origin. Path integration and an environmental cue were both available during the outbound path, but experimental manipulations created single- and dual-cue conditions during the return path. Response variance when returning to the path origin was reduced when both cues were available. These findings indicate that humans integrate multiple spatial cues during navigation. Additionally, participants preferred environmental cues over path integration when cues were placed in a small conflict, while environmental cues were abandoned in favor of path integration cues when cues were placed in a large conflict.

CHAPTER 1. INTRODUCTION

Humans and other animals must navigate to survive. For instance, most animals navigate to find food. To successfully obtain food, animals must remember locations in which they have found food previously and remember how to return to these locations again in the future. In a similar fashion, humans navigate in daily life. We must remember where we are at a given moment, how our location relates to previously visited locations, such as our office, and how to maneuver between these locations. In order for humans and animals to successfully know their location and its relationship to other previously visited locations, a multitude of environmental and internal cues to navigation may be used. This thesis focuses on how multiple cues are combined during navigation.

Two main environmental cues to navigation include geometric cues and landmark cues. Geometric cues are those that can be defined by principles of geometry, which include extended surfaces and angles formed by intersections of surfaces. One example of a geometric cue is room shape. Landmark cues are those which cannot be defined solely by the geometry of extended surfaces, and they are typically more localized than geometric cues. For example, a landmark cue may include a distinctive building on campus or a chair inside of a room.

Two sources of environmental cues may exert differential effects on navigation and spatial memory. Ratliff and Newcombe (2008) examined landmark versus geometric cue use in rooms of different sizes in accordance with the adaptive-combination model of cue use. The adaptive-combination model states that the use of landmark versus geometric cues depends on the relative weight associated with each cue (Newcombe & Huttenlocher, 2006). These relative weights may be determined by cue reliability, validity, and salience as well as previous experience using the cue. To examine the relative use of geometric and landmark cues in small versus large rooms, which may vary in relative weights assigned to the room cue (Sovrano, Bisazza, & Vallortigara, 2007), a cue conflict task was used. As room size increases, the salience and reliability of the room as a cue decreases relative to other available cues, such as landmark cues. Therefore, large rooms should be given less relative weight when compared to small rooms when other available cues remain constant. Participants learned the location of a hidden object in a room (geometric cue) that contained a colored panel (landmark cue) associated with the learned location. After learning the correct location, the colored panel was shifted relative to the room so that the geometric and landmark cues defined conflicting correct locations. Participants were then asked to select a location to search for the hidden object. It was found that the room-indicated location was selected more often in the small room than the large room, indicating that geometric cue weight depends on the size of the room, with the small room receiving more weight than the large room relative to consistent landmark cues.

Internal cues (i.e., cues internal to the navigator), such as path integration, may also be used in navigation. Path integration is the combination of self-motion cues, including vestibular and proprioceptive stimulation, efferent motor commands, and optic and acoustic flow. Path integration accumulates error over time and with movement, such that the greater the walking and turning, the more error occurs in an estimate of location (Klatzky et al., 1990).

Room shape (an environmental cue) and path integration (an internal cue) are combined during human navigation. Kelly, McNamara, Bodenheimer, Carr, and Rieser (2008) demonstrated this cue combination process by having participants navigate in virtual environments viewed on a head-mounted display (HMD). Participants performed a spatial updating task in which they walked paths of varying length before attempting to return to the path origin, and they did so within either a circular virtual room or a square virtual room. The circular room provided no useful geometric cues for spatial updating. The square room, however, contained ambiguous geometric cues: a completely disoriented participant would have only a 25% chance of successful reorientation, but a participant who successfully combined path integration and geometric cues would be able to stay oriented during navigation. As expected, spatial updating errors increased with path length in the circular room, consistent with the notion that path integration is a noisy process subject to cumulative errors (Klatzky et al., 1990). However, spatial updating errors in the square room were small and unaffected by path length, indicating that participants were able to combine the noisy path integration cues with the ambiguous geometric cues in the square room in order to stay oriented during navigation. It was concluded that path integration and room shape were combined to remain oriented in the square room. However, it was unclear exactly how these cues were combined. Kelly et al. (2008) proposed two possibilities for how room shape and path integration cues may be combined based on their results. The first possibility is that participants may have combined path integration and environmental cues continuously during navigation. A second possibility is that participants may have occasionally referenced the square room in order to zero-out any errors that had accumulated in the path integration system.

One approach to studying the integration of multiple cues to navigation involves comparison of human behavior to predictions based on Bayesian principles (Cheng Shettleworth, Huttenlocher, & Rieser, 2007; Nardini, Jones, Bedford, & Braddick, 2008). Bayes' (1763) theorem can be used to determine the optimality with which multiple cues are combined. When provided with two separate cues, either of which could be used to perform the same task, the optimal combination of these cues would be a weighted average in which the weights are inversely proportional to the variance associated with each individual cue. In other words, the more reliable cue (i.e., the one that produces the least response variance) should be weighted more heavily than the less reliable cue. For example, a navigator who walks along a circuitous outbound path before returning directly to the path origin can use both path integration and environmental landmarks to return successfully. However, if the path integration cue would result in greater response variance when returning to the origin than would the landmark cue, then path integration should receive a proportionally lower weight than the landmarks. According to Bayes' (1763) theorem, the optimal weights (*W*) associated with two cues (*X* and *Y*) may be calculated as follows:

$$W_X = \sigma^2{}_Y/(\sigma^2{}_X + \sigma^2{}_Y) \quad (1)$$

$$W_Y = \sigma^2{}_X/(\sigma^2{}_X + \sigma^2{}_Y) \quad (2)$$

Determination of optimal cue weights requires testing participants under single-cue conditions, in order to determine the variances associated with each cue. In the earlier navigation example, this would involve measuring the response variance when returning to the path origin (variance would be assessed across multiple trials) when path integration was the only available cue and when environmental landmarks were the only available cue.

Determination of actual cue weights (which can then be compared to optimal cue weights) requires testing performance in a cue conflict situation (Nardini et al., 2008). In the navigation example, the landmarks could be rotated around the navigator by a sub-threshold amount before the navigator begins the return path. This conflict places the landmark-defined target location in conflict with the path integration-defined target location. When the navigator attempts to return to the origin using cues in conflict, the relative proximity of the response to each cue-indicated correct location indicates the navigator's actual cue weightings. This is calculated as follows:

$$rprox_X = \frac{\frac{1}{d_X}}{\frac{1}{d_y} + \frac{1}{d_X}} = \frac{d_y}{d_y + d_X} \qquad (3)$$

where $rprox_X$ is the response relative proximity to cue X, d_x is the distance of the response from the correct response location indicated by cue X, and d_Y is the distance of the response from the correct response location indicated by cue Y.

When multiple cues are combined, response variance (measured across repeated trials) can be reduced compared to single-cue responses. If the cue weightings are optimal (see Equations 1 and 2), then the response variance when both cues are present is predicted from response variance when only one cue is present, as given by:

$$\sigma^2{}_{X+Y} = w^2{}_Y\sigma^2{}_Y + w^2{}_X\sigma^2{}_X \qquad (4)$$

where w_X and w_Y are the weights given to each cue (which sum to 1). Variance when two cues are present will be less than either of the variances of the single cue conditions and this variance reduction will be greatest when cues are weighted optimally, as determined by Equations 1 and 2. Taken together, these Equations can be used to determine whether humans are combining cues in an optimal fashion.

If individuals do not integrate cues and they instead alternate between cues when the cues are placed in conflict, the variance in their responses may also be predicted (Nardini et al., 2008), as given by:

$$\sigma^2{}_{X+Y} = p_X(\mu^2{}_X + \sigma^2{}_X) + p_Y(\mu^2{}_Y + \sigma^2{}_Y) - (p_X\mu^2{}_X + p_Y\mu^2{}_Y)^2 \quad (5)$$

where $p_X$is the probability of following cue X and $p_Y$is the probability of following cue Y. The probabilities of following each cue sum to unity. The alternation model predicts the variance associated with the probability of following each cue rather than the weight assigned to each cue. The probability of following either cue is calculated using subjects' relative proximity to each cue-indicated correct location. Alternation between cues leads to higher response variance when compared to single-cue conditions because of the separation between cues, and the mean of the mixture of cues is a linear function of their mixture probabilities. Interpreting relative proximity as probability of following each cue, we can determine whether actual variance in responses differs from variances predicted by the model.

Nardini et al. (2008) examined landmark and path integration cue use among children and adults and compared performance to the Bayesian integration model and the alternation model. Adults and children navigated a circular enclosure with only path integration and landmark cues (three unique glowing objects) available. Participants picked up a series of three objects from the floor of the enclosure and then attempted to return to the location of the first retrieved object. In essence, they walked along a two-segment outbound path before attempting to return directly to the path origin. Path integration and landmarks were both available on the outbound path, and experimental manipulations created single-cue (path integration or landmark only) conditions as well as two dual-cue conditions (both cues available and cues put at a 15° conflict) for the return path.

In the path integration only condition, the landmarks were removed so that participants had to rely on path integration alone to attempt to return to the first object location. In the landmark only condition, participants were disoriented (the experimenter repeatedly spun them around in a chair), making path integration an unreliable cue to the previous object location, causing participants to rely on landmark cues alone for the return path. In the cue combined condition, participants were allowed to return to the previously visited location without interference to either the path integration or landmark cues. In the cue conflict condition the landmarks were rotated by 15° in reference to the center of the circular enclosure. Nardini et al. (2008) determined that this 15° landmark rotation was not noticeable to the participants but it placed the path integration indicated correct object location in conflict with the landmark indicated correct object location. Each trial type was repeated four times, so that response variance could be measured across repeated trials. Integration of the landmark and path integration cues should be reflected by lower variance of response locations in conditions in which both cues are present relative to single-cue conditions. Additionally, the relative proximity of participant responses to each cue-indicated locations in the cue conflict condition should reflect the optimal cue weightings predicted from the single cue variances (see Equations 1, 2, and 3). It was found that there was reduced variance for adults in the combined conditions relative to single-cue conditions, but this reduction was not seen for children performing the same task. Additionally, the relative proximity of responses for adults in the cue conflict condition reflected the optimal weightings predicted from the variances in the single-cue conditions using Equations 1 and 2. It was concluded that adults combine landmark and path integration cues in an optimal Bayesian manner while children appear to alternate between cues instead of combining them.

The results of Nardini et al. (2008) indicate that adult humans are able to combine path integration and landmark cues in a Bayesian optimal manner. Additionally, adults use both path integration and room shape when navigating an environment (Kelly et al., 2008). It remains unclear, however, whether this combination of path integration and room shape cues is also optimal in a Bayesian sense. Two possibilities have been proposed by Kelly et al. (2008) regarding how path integration and room shape may be used in navigation. The first possibility is that cues are combined in a Bayesian optimal manner continually during navigation of an environment. The second possibility is that room shape is used to occasionally zero-out accumulating errors in the path integration system during navigation. The present experiments examine whether path integration and room shape cues are used in a Bayesian optimal manner during navigation using methods similar to those used by Nardini et al. (2008).

CHAPTER 2. PILOT STUDY

A pilot study was conducted to examine whether adults optimally combine path integration and room shape. The size of the room was also manipulated between subjects, based on previous research suggesting this manipulation may influence relative cue weights (Ratliff & Newcombe, 2008; Sovrano et al., 2007).

Three predictions were made regarding the results of the pilot study under the assumption that participants would optimally combined room shape and path integration. First, the standard deviation of responses (calculated over repeated trials) will be lower when path integration and room shape are both available, compared to either of the single-cue conditions. Second, responses on cue conflict trials will reflect the optimal cue weights predicted by single-cue conditions. Third, response standard deviations will be higher in the large room than in the small room, and therefore room shape will receive lower relative weighting in the larger room compared to the smaller room due to the reduced reliability of the larger room as a geometric cue for navigation.

Method

Participants

Thirty-five undergraduate students from Iowa State University participated for course credit. Four additional students did not complete the study due to simulator sickness. A trial response was considered outlying if it fell outside of ±2.5 standard deviations from the average response distance from the target location for that participant; 3.4% of total trials were removed as outliers. No participants were removed for multiple outlying responses that would have interfered with calculation of their standard deviation of responses. Participants were assigned to either a large or small room condition. Gender was balanced across conditions.

Stimuli and Design

The virtual environment was displayed on a head-mounted display (HMD; nVisor SX111, NVIS, Reston, VA), which presented stereoscopic images at 1280 x 1024 resolution with 102° horizontal x 64° vertical field-of-view. Images were refreshed at a rate of 60 Hz and reproduced head movement and orientation of the participants as they navigated the virtual environment. In this way, participants were able to physically walk and turn to move through the virtual environment. Vizard software (WorldViz, Santa Barbara, CA) was used to render graphics on a desktop computer with Intel Core2 Quad processors and Nvidia GeForce GTX 285 graphics card.

The virtual environment consisted of a virtual rectangular room that had one wall removed to create a 3-walled room (see Figure 1) presented on an endless grassy plane. There were 16 participants assigned to the small room condition and 19 participants assigned to the large room condition. The room displayed in the small room condition was 4m x 4m and the room displayed in the large room condition was 8m x 8m (Figure 1). Target post locations were displayed in the same physical location, regardless of the size of the virtual room (Figure 1).

Participants were provided with two cues to navigation: the virtual 3-walled room and path integration. For the outbound walking path both cues to navigation were available in all conditions. Participants began each trial standing outside of the 3-walled room at the location of a blue post (blue circle in Figure 1), facing into the virtual room. At the start of a trial, a red target post would appear at one of four locations in the virtual room (red circles in Figure 1). Participants were told that their task was to remember the location of the red target post for the duration of that trial. Participants walked to the target post. When head position data indicated they had reached the location of the target post, the post disappeared and a gray post appeared at one of two locations on the opposite side of the virtual room (e.g., if the target post were on the right side of the room, the gray post would appear on the left side of the room). Participants walked to the gray post and, again, the post disappeared and was replaced by the final gray post when the participant's head position indicated they had reached the correct location. This final gray post was always in the same location in the room, one meter in front of the blue start post. The participants walked to the final gray post and then turned to face the blue start post. When their head position and orientation data indicated that they were at the final gray post and that they were facing the blue start post, the entire virtual world disappeared and was replaced with a gray screen. This gray screen was displayed for 15 seconds and participants were instructed to count backwards from a random start number (provided verbally by the experimenter; e.g., "Count backwards starting at 158") by increments of 3 during that time.

After 15 seconds elapsed, participants attempted to return to the location of the red target post under one of four response conditions. In the path integration (PI) only condition, the virtual ground plane reappeared prior to the participant's response, but the virtual room was absent. Therefore, participants only saw an endless grassy plane and had to rely on path integration cues alone to return to the location of the target post. In the room only condition, participants were spun in place while they counted backwards during the 15 second delay in order to disorient them and render path integration cues unreliable. This disorientation process was modified slightly from the procedure used by Nardini et al. (2008) because of the physical constraints imposed by using the tethered HMD. In the cue combined condition, participants were able to use both the room shape and path integration cues (i.e., the virtual ground plane and room appeared, and they were not disoriented) to attempt to return to the location of the target post. The final condition was the cue conflict condition. To the participants, the cue conflict condition appeared identical to the cue combined condition; however, the virtual room was covertly rotated by 15° during the 15 second delay (during which time the room was not visible). This 15° conflict was not noticeable to the participants (also see Nardini et al., 2008) but it placed the correct target post location indicated by the room shape and the correct location indicated by path integration in conflict. The proximities of participants' responses relative to each of the two cues were later used to determine participants' actual cue weightings. These actual weightings were then compared to the optimal cue weightings calculated from the variances of the single-cue conditions. In each of the four conditions, the primary dependent measure was participants' standing positions when they believed they had reached the target post location.

Participants completed a practice block of trials with each of the four trial types displayed in a predetermined order (cue combined, PI only, room only, cue conflict) followed by four test blocks. Each test block consisted of four trials, one of each trial type in a random order.

Analyses

Because the target location was randomly selected from four possible target locations, participants' responses had to be aligned (rotated and translated) into a single target location prior to analysis. Using the aligned responses, analyses focused on comparison of the standard deviations of participant responses across repeated trials around each participant's own mean response location. Systematic bias in responses does not influence the standard deviation of responses. Initial analyses followed those of Nardini et al. (2008) whereby standard deviations were calculated based on the absolute distance of responses relative to the response mean, and this was calculated separately for each participant. Standard deviation based on absolute distance is insensitive to errors in the X- versus Z-dimension. Scatterplots showing raw responses for each of the four response conditions are shown in Figure 2.

Results

Standard deviations based on absolute response distance (see Figure 3) were analyzed in a mixed-model ANOVA with terms for room size (small or large) and response condition (combined, room only, PI only, and conflict). Only the main effect of condition was significant, $F(3, 99) = 12.42$, $p < .001$, $\eta_p^2 = .27$. The main effect of room size was not significant, $F(3, 99) = 0.81$, $p = .374$, $\eta_p^2 = .02$, nor was the room by condition interaction, $F(3, 99) = 1.84$, $p = .145$, $\eta_p^2 = .27$. These results are described and expanded upon below in the context of the study predictions.

It was predicted that response standard deviations in the room only condition would be lower in the small room compared to the large room. A *t*-test comparing the standard deviation of responses in the small room ($M = 0.22$, $SD = 0.11$) to the standard deviation of responses in the large room ($M = 0.27$, $SD = 0.11$) for the room only condition found no significant difference $t(33) = 1.17$, $p = 0.252$. Taken together with the lack of a significant interaction between room size and condition, there is no evidence that the room size manipulation influenced cue integration. Therefore, data from the small and large rooms were combined for subsequent analyses.

It was predicted that response standard deviation in the cue combined condition would be lower than those in either of the single cue conditions. Planned contrasts revealed that the standard deviation in the cue combined condition was not significantly different from the standard deviation in the room only condition, which was the single cue condition with less variability $F(1, 33) = 0.63$, $p = .433$, $\eta_p^2 = .02$. Furthermore, the interaction contrast comparing condition (cue combined vs. room only) and room size (small vs. large) was not significant, $F(1, 33) = 0.86$, $p = .360$, $\eta_p^2 = .03$. The cue conflict condition was also not significantly different from the room only condition $F(1, 33) = 0.001$, $p = .980$, $\eta_p^2 = .00$ and the interaction contrast comparing condition (cue conflict vs. room only) and room size (small vs. large) was not significant, $F(1, 33) = 0.66$, $p = .422$, $\eta_p^2 = .02$. In summary, standard deviations of responses in the dual-cue conditions (cue combined or cue conflict) were no different than those in the best single-cue condition (room only), which suggests that participants may not have optimally combined room shape and path integration. These results are again illustrated in Figure 3.

The results based on absolute errors were not as expected so exploratory analyses examined contrasts in the X- and Z-dimensions independently. Due to the exploratory nature of these analyses, the more conservative value of $p = .01$ was used as the indicator of significance. The X-dimension of the room refers to distance in width of the room while the Z-dimension is the distance in the length of the room when viewed from the starting location on each trial (Figure 1). When examining the possible target locations, it is clear that the distribution of locations differs between the X- and Z-dimensions. In the X-dimension, the target locations vary across the width of the room, with some locations occurring close to the virtual room walls. In the Z-dimension, in contrast, the target locations vary little and remain farther from room walls. To examine possible differential effects depending on the room dimension, standard deviations of responses were calculated based on the X- and Z-dimensions independently (Figure 4). For example, if the participant's mean response location was (X = 0, Z = 0) and the participant's response location on a given trial was (0.3, 0.5), their X-dimension distance from the target location for that trial would be 0.3, or (0.3 – 0), and their Z-dimension distance from the target location for that trial would be 0.5, (0.5 – 0). Across trials, the standard deviation of these distances in each dimension was calculated.

To examine whether the room only condition differed from either of the dual-cue conditions in the X-dimension, which would indicate integration of cues, contrasts compared the room only condition to each of the dual-cue conditions. Contrasts comparing the room only condition to the cue combined condition in the X-dimension found no significant difference $F(1, 33) = 1.85$, $p = .183$, $\eta_p^2 = .05$ and no interaction between condition and room size $F(1, 33) = 0.23$, $p = .602$, $\eta_p^2 = .01$. Contrasts comparing the room only condition to the cue conflict condition in the X-dimension also found no significant difference $F(1, 33) = 0.65$, $p = .426$, $\eta_p^2 = .02$ and no interaction between condition and room size $F(1, 33) = 0.21$, $p = .647$, $\eta_p^2 = .01$. Thus, there were no significant effects discovered in the X-dimension of responses.

Contrasts comparing the room only condition to the combined condition in the Z-dimension found no significant main effect of condition $F(1, 33) = 0.38$, $p = .541$, $\eta_p^2 = .01$ and did not find a significant interaction between condition and room size, due to the more conservative significance value of p = .01 $F(1, 33) = 4.90$, $p = 0.034$, $\eta_p^2 = .13$. Contrasts comparing the room only condition to the cue conflict condition in the Z-dimension found a significant main effect of condition $F(1, 33) = 15.40$, $p < .001$, $\eta_p^2 = .32$ but no interaction between condition and room size $F(1, 33) = 2.37$, $p = .133$, $\eta_p^2 = .07$.

Discussion

The first prediction was that the cue-combined conditions would have significantly lower standard deviation of responses than the single-cue conditions. This prediction was only supported in the Z-dimension comparison between the conflict condition and the room only condition. One possible explanation for the difference between the X- and Z-dimension results could be the post locations used in this study. The post locations were closer to the walls in the X-dimension than they were to walls in the Z-dimension. It could be that having only four possible post locations that were all fairly close to the walls in the X-dimension made integration in that dimension unnecessary, while integration was required in the Z-dimension because of the increased difficulty in having the posts farther from room walls. This explanation does not explain the differences in results between the conflict and combined cue conditions, however.

The second prediction of the pilot study was that responses on cue conflict trials would reflect the optimal cue weightings predicted by the single-cue conditions. This prediction was inconclusive. There was no significant difference between the standard deviations in the cue-combined condition and the room shape only condition. For this reason, it is unclear whether the participants integrated the two cues to navigation. Without integration, the relative proximities of participant responses to each of the cue indicated correct locations are not informative about participants' actual cue weightings. Thus, the analysis of cue weight optimality was not conducted.

The third prediction of the pilot study was that room shape would receive lower weighting in the larger room compared to the smaller room due to reduced reliability. This prediction was not supported by the analyses. One explanation for inconsistent results compared to previous research could be due to the differences in room sizes used. The size of the room in the small room condition of the current experiment was similar to the large room condition used by Newcombe et al. (2008). Experiment 1 further examined the current small room and large room conditions with modified stimuli (post locations) and a larger sample size.

CHAPTER 3. EXPERIMENT 1

The results of the pilot study, while encouraging, were inconclusive for the hypotheses of interest. Experiment 1 made one main change to improve on the pilot study and further examine cue integration between room shape and path integration in rooms of different sizes. This change was the addition of ten more target post locations, for a total of fourteen possible target post locations for each trial (Figure 5). The additional target posts should make it more difficult for participants to memorize the four possible target positions from the pilot study. Additionally, this experiment recruited additional participants for a total of 48 to increase the power to detect the small differences between conditions.

Method

Participants

The estimated effect size from the paired *t*-test comparing the landmark only condition to the cue combined condition in the experiment conducted by Nardini et al. (2008) was used to estimate a priori power for experiment 1. The results of Nardini et al. (2008) were used for power analysis rather than the results of the pilot study because no evidence of integration was found in the pilot study. Therefore, the stimuli were altered (more post locations were added) from the pilot study to experiment 1 to increase the likelihood of integration. A power analysis using the Gpower computer program (Faul, Erdfelder, Lang, & Buchner, 2007) indicated that a total sample of 8 people would be needed to detect the effect with 80% power using a planned contrast with alpha at .05 and a correlation between means of 0.5.

Forty-eight undergraduate students from Iowa State University participated for course credit. Two additional students did not complete the study due to simulator sickness. A trial response was considered outlying if it fell outside of ±2.5 standard deviations from the average response distance from the target location for that participant; 7.5% of total trials were removed as outliers. Two participants were removed from analyses because of multiple outlying responses that prevented the calculation of accurate standard deviations of responses. Participants were assigned to either a large or small room condition. Gender was balanced across conditions.

Stimuli and Design

The stimuli and design of experiment 1 were identical to that of the pilot study with one modification. Instead of four possible target post locations there were fourteen target post locations in experiment 1. These target post locations were all equidistant from the start post, arranged in an arc formation.

Results

Responses were transformed to align to a single location instead of fourteen possible target locations for the analyses. Standard deviations of participant responses across repeated trials were recorded. Scatterplots showing raw responses for each of the four response conditions are shown in Figure 6.

Standard deviations based on absolute response distance (see Figure 7) were analyzed in a mixed-model ANOVA with terms for room size (small or large) and response condition (combined, room only, PI only, and conflict). The only significant effect was a main effect of condition $F(3, 132) = 10.11$, $p < .001$, $\eta_p^2 = .19$. There was no significant room by condition interaction in the absolute distance of responses from the target location $F(3, 132) = 0.33$, $p = .805$, $\eta_p^2 = .07$, there was also no significant main effect of room $F(1, 44) = 1.48$, $p = .230$, $\eta_p^2 = .03$. These results are displayed in Figure 7.

It was predicted that response standard deviation would be lower in the small room compared to the large room in the room only condition. A *t*-test comparing the standard deviation of responses in the small room (M = 0.26, SD = 0.10) to the standard deviation of responses in the large room (M = 0.28, SD =0.14) for the room only condition found no significant difference $t(44) = 0.67$, $p = 0.506$. Because there was no significant interaction between room size and condition and there was also no significant difference between the two room sizes in the room only condition, there is no evidence that the small and large room manipulation had an effect on response standard deviations. Therefore, data from the small and large rooms were combined for all subsequent analyses.

Planned contrasts revealed that response standard deviations in the room only condition were significantly higher than in the combined condition $F(1, 44) = 11.67$, $p = .001$, $\eta_p^2 = .21$ and there was no significant interaction between the conditions of interest and room size $F(1, 44) = 0.01$, $p = .927$, $\eta_p^2 = .00$. Response standard deviations in the room only condition were also significantly higher than the conflict condition $F(1, 44) = 4.12$, $p = .048$, $\eta_p^2 = .09$ and there was no significant interaction between condition and room size $F(1, 44) = 0.25$, $p = .619$, $\eta_p^2 = .01$. Together, these results indicate that participants combined room shape and path integration in order to reduce response variance when multiple cues were available (i.e., in the combined and conflict conditions), compared to single cue conditions.

The second prediction was that responses on cue conflict trials would reflect the optimal cue weightings predicted by single-cue conditions. Optimal weights for the room shape and path integration cues were calculated for each participant using variances from each of the single cue conditions following Equations 1 and 2. Actual weights for room shape and path integration were calculated as the relative proximity of responses to the room-defined and path integration-defined locations on conflict trials following Equation 3. A paired-samples *t*-test compared the calculated optimal weight for the room shape cue for each individual participant to their actual room shape weighting. The optimal room weight (M = 0.55, SD = 0.26) and the actual room weight (M = 0.57, SD = 0.07) were not significantly different $t(45) = 0.62$, $p = .536$, 95% CI [-0.05, 0.10], suggesting that participants optimally weighted path integration and room shape in the cue conflict condition.

To determine whether there was a significant preference for the room shape cue over the path integration cues in the conflict condition, the relative proximity of responses to the room shape-indicated correct location was compared to 0.5, which would be the relative proximity of responses if neither cue was preferred over the other. A one-sample *t*-test indicated that the room shape cue received a significantly higher weight (M = 0.57, SD = 0.07) than 0.5, $t(45) = 6.61$, $p < .001$.

Figure 8 illustrates the comparison of the actual room weight and standard deviation of the conflict condition responses to the Bayesian model predictions. The model shows predicted response standard deviation (using Equation 4) given different possible weightings of the two cues. The minimum y-value represents optimal performance given optimal cue weights. Each individual has their own model prediction curve, actual room weight, and standard deviation of responses in the conflict condition and therefore each participant could have their own figure. Figure 8 uses the average room weights and standard deviations to display an average of the individual curves. A paired-samples *t*-test compared each individual's actual standard deviation of responses in the conflict condition to the standard deviation predicted using their actual cue weights and Equation 4. There was no significant difference between the actual standard deviation of responses (M = 0.23, SD = 0.11) and the predicted standard deviation of responses

(*M* = 0.22, *SD* = 0.09), *t*(45) = 0.44, *p* = .662, 95% CI [-0.03, 0.05], suggesting that participants optimally combined room shape and path integration.

Although there were no significant differences between the actual cue weight and optimal cue weight or between the actual standard deviation of responses in the conflict condition compared to the predicted standard deviation of responses, it is difficult to make theoretical conclusions on non-significant null-hypothesis tests. However, it is important to make theoretical conclusions based on equivalence of observations (Gallistel, 2009). Therefore, we also subjected these comparisons to Bayesian analyses. Unlike null hypothesis testing, these analyses can be used to determine evidence in support of the null hypothesis (Gallistel, 2009). As displayed in Table 1, results supported the equivalence of actual and optimal cue weights as well as actual standard deviation of responses and predicted standard deviation of responses in the cue conflict condition.

Discussion

Response variance when returning to the path origin was reduced when both cues were available. Additionally, responses on cue conflict trials reflected the optimal weightings predicted by the single cue conditions. These findings suggest that humans integrate room shape and path integration cues during navigation, and that this integration is optimal.

Contrary to prediction and inconsistent with previous work, experiment 1 showed no significant difference in the standard deviation of responses when comparing the small room condition to the large room condition. One explanation for the inconsistent results could be differences in room sizes used in previous studies. The size of the room in the small room condition of the current experiment was similar to the large room condition used by Newcombe et al. (2008). The size of the small room used in the current studies was chosen to remain as similar as possible to Nardini et al. (2008). The distance between the participants to the walls of the virtual room used in the current studies was equivalent to the distance between the participants and the landmark cues used by Nardini et al. (2008). Doubling the size of the small room to create the large room allowed for the target posts to remain in the same physical locations regardless of the room size condition.

The significant reduction of response standard deviations in the cue combined compared to the room only condition indicates that participants combined path integration and room shape cues when navigating in the virtual environment. Additionally, further analyses showed no significant difference in response standard deviation of the cue conflict condition when compared to the optimal standard deviation predicted using the single cue conditions. This suggests that participants were optimally combining the cues to reduce variance in navigation. These results mirror the optimal combination of landmark and path integration cues found by Nardini et al. (2008).

Including additional possible target post locations in experiment 1 was intended to make the room only condition relatively more difficult when compared to the combined condition. It appears the additional posts succeeded in increasing the difficulty because there was evidence of integration when comparing standard deviations in the cue combined and room only conditions. This is in contrast to the results of the pilot study where fewer target post locations were used and there was no evidence of cue integration.

Experiment 1, along with the results of Nardini et al. (2008), indicates that humans optimally combine landmark and room shape cues with path integration cues when navigating an environment. Additionally, participants appear to favor the environmental cues, which tend to produce the lowest response variance, over the path integration cues when the two cues are placed in small conflict, as illustrated by the relative proximity of responses to each of the conflicting cue-indicated correct target locations. Animals studies (Chittka & Geiger, 1995; Shettleworth & Sutton, 2005; Wehner, Boyer, Loertscher, Sommer, & Menzi, 2006; Wehner, 2003) have revealed that this preference for environmental over egocentric cues to navigation may not persist when cues are placed in a large conflict (e.g., when the landmarks are rotated by a supra-threshold amount). Experiment 2 attempted to connect animal research on cue conflict to human research on cue integration by investigating cue integration under sub- and supra-threshold conflict conditions.

CHAPTER 4. EXPERIMENT 2

Experiment 2 again examined the use of multiple cues during navigation. The purpose of the second experiment was to connect animal studies examining cue competition with large cue conflicts to adult human studies that examine cue integration and small cue conflicts, such as the pilot study and experiment 1.

Animal studies have shown that environmental cues, such as beacons (Shettleworth & Sutton, 2005) and landmarks (Chittka & Geiger, 1995; Kohler & Wehner, 2005; Wehner, Michel, & Antonsen, 1996; Whishaw & Tomie, 1997) may be preferred cues over path integration when an animal must return to a previously visited location and the cues are in a small conflict. However, environmental cues may be abandoned and path integration preferred for large conflicts (Chittka & Geiger, 1995; Shettleworth & Sutton, 2005; Wehner et al., 2006; Wehner, 2003). These seemingly contradictory results lead to a hypothesis that path integration may function as a back-up system for navigation and may be reconciled with Bayesian principles (see Cheng et al., 2007 for review).

In one experiment using rats, Shettleworth and Sutton (2005) compared the preference rats assigned to beacons, which are landmarks coincident with the target location, and path integration in conflict conditions. Rats were trained to find a food pellet in a circular arena and return to eat it in their home box. The home box was attached to the arena through one of several possible doors, evenly spaced around the arena. In some conditions, a single visible beacon (black panel surrounding the door) indicated the correct home door during learning. When the beacon was present during learning, the home location was redundantly signaled by the beacon and by path integration. During subsequent testing, when the beacon was offset by 45° from the correct door (i.e., the beacon was placed in conflict with path integration), the rats travelled to the beacon-indicated door first, ignoring path integration. When the beacon was offset by 90°, however, half of the rats ignored it completely and followed path integration to the correct door and the other half of the rats continued to prefer the beacon indicated correct door. This indicates that with a 90° conflict between the beacon and path integration cues, different rats appear to solve the discrepancy differently, while the vast majority of the rats chose the beacon-indicated correct door when there was a small conflict between cues. When there was no beacon present, those rats that initially learned with the beacon performed as accurately as those who learned with no beacon present or with an unreliable beacon present. In summary, 1) rats learned to return home using both the beacon and path integration, 2) the vast majority of rats preferred the beacon when the cue conflict was small, and 3) half of the rats preferred path integration when the conflict was large. This has led some to suggest that path integration can serve as a back-up system, relied upon when other cues seem unreliable.

While environmental cues may be abandoned for path integration cues when there is a large conflict, this may not always be the case depending on the nature of the environmental cues. In contrast to the results of the single-beacon experiment reported by Shettleworth and Sutton (2005), it has been found that rats do not abandon the conflicting environmental cues in favor of path integration when there are many environmental cues (Olton & Samuelson, 1976; Suzuki, Augerinos, & Black, 1980). Suzuki et al. (1980) showed that rats prefer multiple landmark cues over path integration cues when they are placed in a large conflict. Rats learned to gather food from each of eight arms in a radial maze with multiple landmark cues provided. In one experiment, rats were closed in the center platform of the maze after collecting food from 3 of the 8 arms. While the rats were confined to the center, the center platform was covered with a lid that prevented the rats from seeing the manipulation and the radial arms and landmarks were rotated by 180° around the rat. When rats were again allowed to search for the food at the remaining 5 baited arms, they followed the landmark configuration rather than path integration indicated correct arms. One possible reason that rats followed the landmarks to resolve a large conflict in the Suzuki et al. (1980) study but followed path integration in the Shettleworth and Sutton (2005) study is that there were many more landmark cues (and all were rotated by the same amount) in the Suzuki et al. (1980) study.

Geometric cues tend to be favored over landmark or path integration cues to navigation in rats (Cheng, 1986). Rats are highly sensitive to room shape, but often fail to incorporate disambiguating featural cues. This may indicate that geometric cues will tend to be weighted more heavily than landmark or path integration cues to navigation when integrating cues. When geometric cues are placed in a large conflict with path integration cues, the geometric cue may continue to be favored over the path integration cue, similar to the results found when multiple landmark cues are placed in conflict with path integration cues.

This pattern of responses in conflict conditions, such that single landmark cues are preferred over path integration for small conflicts, but not for large conflicts, and that especially stable environmental cues, such as multiple landmarks and room shape, continue to be preferred over path integration for large conflicts can be reconciled using Bayesian logic (see Cheng et al., 2007). Because path integration is entirely motion-based, error accumulates during self-motion. When there is a small conflict between a single landmark cue and path integration cues, the path integration cue may be in error, making the landmark cue the most accurate indicator of the target location. Thus, for small conflicts comparing path integration to a single landmark, the landmark would be the preferred target location predictor. However, though path integration is an error-prone system, it is also unambiguous. In a natural environment, landmarks may be moved or there may be multiple similar landmarks (such as trees). Thus, if there is a large conflict between path integration and a single landmark, the landmark may be in error and path integration will be relied upon because it is unambiguous. When multiple landmarks are present, such as trees in a forest, and are in large conflict with path integration, it will instead become improbable that the entire set of landmark cues shifted together to be in error. Instead, it is more likely that the navigator became disoriented and path integration should be abandoned in favor of the multiple landmarks.

It was hypothesized that when adult humans must respond in conditions of small conflict between cues they will combine cues and will give higher weighting to environmental cues compared to path integration. Increased weighting of room shape over path integration shown in experiment 1, indicating a preference for environmental cues when given a small conflict, is consistent with animal conflict research (Shettleworth & Sutton, 2005). When there is a large conflict between cues, it was hypothesized that one landmark alone will be abandoned in favor of path integration. However, when multiple landmarks in an array or room shape are placed in large conflict with path integration, it was hypothesized that participants will continue to prefer the environmental cues over path integration.

Method

Participants

The effect size from the planned contrast comparing the room only condition to the cue combined condition in experiment 1 was used to calculate a priori power for experiment 2. A power analysis using the Gpower computer program (Faul et al., 2007) indicated that a total sample of 32 people would be needed to detect the effect with 80% power using a planned contrast with alpha at .05.

Sixty Iowa State University undergraduate students participated in exchange for course credit. Twenty nine additional students did not complete the study due to simulator sickness. The high rate of simulator sickness related attrition is likely due to the additional trials in experiment 2 and due to using more conservative criteria for ending experiments when participants reported symptoms of simulator sickness. With extended exposure to virtual environments, close to 50% of people will experience some form of simulator sickness (Kennedy, Lane, Berbaum, & Lilienthal, 1993). Because of the increased length of experiment 2, stricter criteria were used to eliminate participants who indicated symptoms of simulator sickness. Participants who reported simulator sickness symptoms within or immediately following the block of practice trials were excluded from completing the experiment, because it was assumed that many would eventually experience more severe symptoms and drop out of the study.

A trial response was considered outlying if it fell outside of ±2.5 standard deviations from the average response distance from the target location for that participant, there was no attempt to remove outliers in the large conflict condition; 2.0% of total trials were removed as outliers. No participants were removed because of multiple outlying responses preventing calculation of standard deviations of responses.

Participants were assigned to three between-subjects cue conditions: room, one landmark, and three landmarks. There were 20 participants in each of the three environmental cue conditions. Gender was balanced across conditions.

Stimuli and Design

Experiment 2 included three between-subjects environmental cue conditions: one landmark, three landmarks, and room shape (Figure 9). In the one landmark condition, participants completed the experiment with one landmark used as an environmental cue instead of the room shape cue used in the previous experiments. In the three landmark condition, participants experienced three landmarks in an array instead of room shape, arranged as the landmarks used by Nardini et al. (2008). In the room shape condition, participants experienced the small room cue used in the previous experiments; there was no manipulation of room size in experiment 2.

The task required of participants was similar to that of the pilot study and experiment 1. Participants again navigated from a start location to a target post, then to two more posts, and then attempted to navigate back to the location of the target post under conditions of differing cue manipulations. For the return trip, experiment 2 included the four conditions previously used (cue combined, room only, path integration only, and cue conflict) and additionally included a large cue conflict condition. In the large cue conflict condition the environmental cue was rotated by a noticeable amount, 90°[1].

Results

Participant responses were transformed to align to a single location instead of fourteen possible target locations for the analyses. Standard deviations of participant responses across repeated trials were recorded. Scatterplots showing raw responses for each of the five response conditions are shown in Figure 10.

Standard deviations based on absolute response distance (see Figure 11) were analyzed in a mixed-model ANOVA with terms for cue type (room, one landmark, or three landmarks) and response condition (combined, environmental cue only, PI only, small conflict, and large conflict). There was no significant cue by condition interaction in the absolute distance of

[1] Pilot testing of various rotation angles revealed that the majority of participants noticed a 90° rotation of the environmental cue.

responses from the target location $F(8, 228) = 1.11$, $p = .354$, $\eta_p^2 = .04$, there was also no significant main effect of cue type $F(2, 57) = 2.70$, $p = .076$, $\eta_p^2 = .09$. There was a main effect of condition $F(4, 228) = 20.16$, $p <.001$, $\eta_p^2 = .26$.

It was predicted that the room cue would produce lower standard deviation in response locations in the room shape cue condition compared to the three landmarks cue, which would also produce lower standard deviation in response locations compared to the one landmark cue. An ANOVA comparing the standard deviation of responses in the room cue condition ($M = 0.37$, $SD = 0.26$) to the standard deviation of responses in the three landmark condition ($M = 0.38$, $SD =0.24$) and in the one landmark condition ($M = 0.49$, $SD =0.30$) for the environmental cue only condition found no significant effect of environmental cue type $F(2, 57) = 1.23$, $p = 0.301$, $\eta_p^2 = .04$. Because there was no significant interaction between environmental cue and condition and there was also no significant difference between the standard deviations of the cues in the environmental cue only condition, there is no evidence that the cue manipulation had an effect on cue integration. The cues were combined for further integration analyses.

Planned contrasts revealed that standard deviations of responses in the environmental cue only condition were significantly higher than in the combined condition $F(2, 57) = 32.41$, $p = .001$, $\eta_p^2 = .36$ and there was no significant interaction between the conditions of interest and cue type $F(2, 57) = 0.13$, $p = .882$, $\eta_p^2 = .00$. Standard deviations in the environmental cue only conditions were not significantly different than those in the small conflict condition $F(2, 57) = 0.68$, $p = .414$, $\eta_p^2 = .01$ and there was no significant interaction between condition and cue type $F(2, 57) = 0.11$, $p = .896$, $\eta_p^2 = .00$.

It was predicted that responses on small conflict trials would reflect the optimal cue weightings predicted by single-cue conditions. Optimal weights for the environmental cues and path integration cues were calculated using variances from each of the single cue conditions following Equations 1 and 2. A paired-samples *t*-test compared the calculated optimal weight for the environmental cue for each individual participant to their actual environmental cue weighting (i.e., the relative proximity of their response locations to the environmental cue indicated correct target location in the small conflict condition). The optimal weight (*M* = 0.58, *SD* = 0.28) and the actual weight (*M* = 0.53, *SD* = 0.09) were not significantly different *t*(59) = 1.30, *p* = .199, 95% CI [-0.13, 0.03].

Figures 12 and 13 illustrate the comparison of the actual environmental cue weight and standard deviation of the conflict condition responses to the Bayesian model predictions. The model shows predicted response standard deviation (using Equation 4) given different possible weightings of the two cues. The minimum y-value represents optimal performance given optimal cue weights. Each individual has their own model prediction curve, actual environmental cue weight, and standard deviation of responses in the conflict condition and therefore each participant could have their own figure. Figures 12 and 13 use the average environmental cue weights and standard deviations to display an average of the individual curves. A paired-samples *t*-test compared each individual's actual standard deviation of responses in the small conflict condition to the standard deviation predicted using their actual cue weights and Equation 4. There was no significant difference between the actual standard deviation of responses (*M* = 0.38, *SD* = 0.19) and the predicted standard deviation of responses based on actual cue weighting (*M* = 0.35, *SD* = 0.16), *t*(59) = 1.08, *p* = .283, 95% CI [-0.03, 0.09], suggesting that participants optimally combined environmental cues and path integration.

Although there were no significant differences between the actual cue weight and optimal cue weight or between the actual standard deviation of responses in the small conflict condition and the predicted standard deviation of responses, it is difficult to make theoretical conclusions on non-significant null-hypothesis tests. Therefore, we also subjected these comparisons to Bayesian analyses (Gallistel, 2009). As displayed in Table 1, results supported the equivalence of actual and optimal cue weights as well as actual standard deviation of responses and predicted standard deviation of responses in the small cue conflict condition.

An ANOVA comparing the relative proximity of responses to the environmental cue defined correct location in the large conflict condition across the three cue types, room cue condition (M = 0.41, SD = 0.22), three landmark condition (M = 0.34, SD =0.17) and one landmark condition (M = 0.30, SD =0.15), found no significant effect of environmental cue type $F(2, 57) = 1.99$, $p = 0.146$, $\eta_p^2 = .07$. Because there was no significant effect of cue type on relative proximity to the environmental cue in the large conflict condition, these data have been combined in the model figure and in further analyses of the large conflict condition.

A prediction for the large conflict condition was that participants would no longer integrate cues when there is a noticeable conflict and would instead choose one cue over another. A paired-samples *t*-test compared the calculated optimal weight for the environmental cue for each individual participant to their actual environmental cue weighting based off of the relative proximity of their response locations to the environmental cue-indicated correct target location. The optimal weight (M = 0.58, SD = 0.28) and the actual weight (M = 0.35, SD = 0.19) were significantly different in the large conflict condition $t(59) = 6.21$, $p < .001$, 95% CI [-0.31, -0.16].

A paired-samples *t*-test compared each individual's actual standard deviation of responses in the large conflict condition to the standard deviation predicted using their actual cue weights and Equation 4. There was a significant difference between the actual standard deviation of responses (*M* = 0.57, *SD* = 0.37) and the predicted standard deviation of responses based on actual cue weighting (*M* = 0.36, *SD* = 0.17), $t(59) = 4.47$, $p < .001$, 95% CI [0.12, 0.31], suggesting that participants did not optimally combine environmental cues and path integration in the large conflict condition.

To evaluate whether preference for environmental or path integration cues differed between large and small conflicts, a paired-samples *t*-test compared each individual's relative proximity to the environmental cue-defined correct location in the large conflict condition (*M* = 0.35, *SD* = 0.19) and their relative proximity to the environmental cue-defined correct location in the small conflict condition (*M* = 0.53, *SD* = 0.09). In the small conflict condition, participants responded significantly closer to the cue-defined correct location than they did in the large conflict condition, $t(59) = 7.41$, $p < .001$.

To evaluate whether there was a significant preference for either the path integration or environmental cue in the small and large conflict conditions, a one-sample *t*-test compared the average relative proximity to the environmental cue-defined correct location in the small conflict condition and in the large conflict condition to 0.5, which would be the relative proximity if neither cue was preferred over the other. The relative proximity of the small conflict condition (*M* = 0.53, *SD* = 0.09) was significantly higher than 0.5, $t(59) = 2.79$, $p = .007$. The relative proximity of the large conflict condition (*M* = 0.35, *SD* = 0.19) was significantly lower than 0.5, $t(59) = 6.18$, $p < .001$. Together, these results indicate that the environmental cue is preferred over the path integration cue in the small conflict, but the path integration cue is preferred over the environmental cue in the large conflict condition,

Discussion

Experiment 2 largely mirrored the results of experiment 1 with regard to the integration of cues. However, the comparison of standard deviations of responses in the small conflict condition compared to the standard deviations of responses in the cue only condition did not reach statistical significance. This could be evidence that participants were not combining cues in a fully optimal fashion in the small conflict condition. Significantly reduced standard deviation of responses in the cue combined condition compared to the environmental cue only condition indicates that participants were integrating path integration and environmental cues when navigating in the virtual environment in the combined condition. Additionally, participants' actual cue weights were not significantly different from predicted cue weights, suggesting that participants optimally combined the cues to reduce variance in navigation.

The two primary hypotheses of interest in experiment 2 were that (1) participants would prefer environmental cues over path integration cues in a small conflict, but that this preference would be reversed when there is a large conflict between cues and, (2) the environmental cues of room shape and multiple landmarks, but not the single landmark, would continue to be preferred over path integration in a large conflict. Our results indicate that there were no differential effects of cue type (room shape, single and multiple landmarks) on cue preference in the conflict conditions but there was a significant shift from preferring the environmental cue in the small conflict condition to preferring path integration in the large conflict condition.

It was predicted that the environmental cues of room shape and multiple landmarks would be perceived as more stable than a single landmark and would therefore continue to be preferred over path integration in a large conflict, consistent with previous animal research (Olton & Samuelson, 1976; Suzuki, Augerinos, & Black, 1980). However, adding the large conflict condition in the present experiment probably indicated to the participants that the environmental cue was not completely stable. In rats, experience with an unreliable cue caused head direction (HD) cells, which respond to the head direction of the rats, to fire differently in response to a rotated (i.e., conflicting) cue than HD cells in rats without such experience (Knight et al., 2014). HD cells in rats experienced with conflicting cues increasingly under-rotated with greater conflict in cues, while HD cells in rats that experienced a similar degree of conflict without prior exposure to the conflicting cues showed much less under-rotation. In a similar study, adult humans learned a navigation shortcut with landmarks present (Foo, Warren, Duchon, & Tarr, 2005). When these landmarks were shifted by a small amount, participants followed the landmarks in their navigation routes. However, when landmarks were shifted by a large amount and this shift was noticed by participants, those participants who noticed the shift did not follow the cue and, in fact, seemed to completely ignore the landmarks and instead used other navigation strategies.

In the present experiment, participants were aware from the practice block that the environmental cue was not entirely stable and would move sometimes throughout the experiment. Perceiving the environmental cue as being unreliable may have prevented participants from following the environmental cue that might have otherwise been perceived as stable without prior experience with large conflicts. Future research should examine adult human responses to large conflicts when they have no prior knowledge of the environmental cue being unstable. Under those conditions, particularly stable cues, such as multiple landmarks and room walls, might be preferred in a large conflict whereas path integration might be preferred in large conflicts with less stable environmental cues, such as one landmark.

The present experiment found a significant difference between actual cue weighting in the small and large conflict conditions. In the small conflict condition, participants responded closer to the environmental cue-indicated correct post location, while in the large conflict they responded closer to the path integration-indicated correct post location. This is consistent with previous research using animals (Chittka & Geiger, 1995; Shettleworth & Sutton, 2005; Wehner et al., 2006; Wehner, 2003).

Experiment 2 provides further support to the findings of experiment 1 and those of Nardini et al. (2008); adult humans combine environmental cues such as room shape and landmarks with path integration cues in a Bayesian optimal manner. Additionally, experiment 2 indicated that, consistent with research involving animals, adult humans may abandon environmental cues, which are favored in small conflicts, for path integration cues when the conflict between cues is large. This is consistent with the hypothesis that path integration may function as a backup system for navigation (see Cheng et al., 2007 for review). Experiment 2 failed to find an effect of cue type on environmental cue preference in the large conflict condition, contrary to prediction. This result may have been due to experimental procedures resulting in all environmental cues being perceived by participants as unstable.

CHAPTER 5. GENERAL DISCUSSION

The results of the present experiments extend our understanding of cue combination during human navigation. Previous research has indicated that humans combine room shape and path integration cues when they navigate in an environment (Kelly et al., 2008); however, it was unclear how this combination of cues occurred. Additionally, geometric cues, such as room shape, have been found to exert different effects on navigation than landmark cues (Newcombe & Huttenlocher, 2006; Ratliff & Newcombe, 2008). Bayesian optimal combination of landmark and path integration cues has been found in adult humans (Nardini et al., 2008). Previous to the current studies, it was unclear whether geometric cues, such as room shape, and path integration cues were combined in an optimal fashion.

Experiments 1 and 2 provide evidence that adult humans optimally combine geometric cues, such as room shape, and path integration cues. Additionally, experiment 2 mirrors the finding of Nardini et al. (2008) that landmark and path integration cues are combined in a Bayesian optimal manner. The current experiments also show a preference for environmental cues in a small conflict between an environmental cue and path integration cues. This is reflected in the relative proximity of responses to the environmental cue-indicated correct location in small conflicts of 15°.

Research conducted with animals, such as rats, has also found a preference for environmental cues in small conflict, however, these animals often abandon the environmental cues for path integration in large conflicts (Chittka & Geiger, 1995; Shettleworth & Sutton, 2005; Wehner et al., 2006; Wehner, 2003). Experiment 2 extended these results to adult humans by finding a preference for environmental cues in conditions of small conflict and a preference for path integration cues when cues are in a large conflict.

While animal research has found that environmental cues are abandoned in favor of path integration cues in conditions of large conflicts between cues, this may not be the case when the environmental cue is especially stable (Olton & Samuelson, 1976; Suzuki, Augerinos, & Black, 1980). One hypothesis of experiment 2 was that participants would not abandon the environmental cues of room shape and multiple landmarks, because it was believed they would be perceived as more stable cues than a single landmark. This hypothesis was not supported; there was no significant difference in cue weightings across environmental cue condition. This may have been due to the nature of the experimental methods, which may have caused all environmental cues to be perceived as unstable (see Knight et al., 2014).

This pattern of responses in conflict conditions, such that single landmark cues were preferred over path integration for small conflicts, but not for large conflicts, can be reconciled using Bayesian logic (see Cheng et al., 2007). Path integration accumulates error over time. When there is a small conflict between a single landmark cue and path integration cues, the path integration cue may be in error, making the landmark cue is the most accurate indicator of the target location. However, though path integration is an error-prone system, it is also unambiguous. In a natural environment, landmarks may be moved or there may be multiple similar landmarks (such as trees). Thus, if there is a large conflict between path integration and a landmark, the landmark may be in error and path integration will be relied upon because it is not ambiguous. This is consistent with the hypothesis that path integration may function as a backup system for navigation.

The results of the present studies indicate that adult humans can optimally combine the geometric cue of room shape and path integration cues to navigate. Additionally, experiment 2 extends navigation research from animal studies to humans by showing humans have a preference for following environmental cue-indicated correct locations in small conflicts but will abandon environmental cues in favor of the path integration-indicated correct locations in large conflicts.

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Table 1

Bayesian analyses including odds in favor of the null hypothesis and weight for the equivalence of cue weights and condition standard deviations for each experiment. *P*-values from standard null hypothesis testing using paired-samples *t*-tests are included.

Experiments	**Comparison**	**Odds in favor of the null**	**Weight**	***P*-value**
Experiment 1	Optimal/Actual Cue Weight	8.4:1	-0.92	.54
	Actual/Predicted SD for Conflict	8.3:1	-0.92	.66
Experiment 2	Optimal/Actual Cue Weight	3.7:1	-0.57	.20
	Actual/Pred. SD Small Conflict	6.4:1	-0.80	.28

Note. Odds < 3:1 are considered “weak”; Odds between 3-10:1 are considered “substantial”; Odds between 10-100:1 are considered “strong”; Odds > 100:1 are considered “decisive”. Weights are evaluated based on their absolute values. Weights < 0.5 are considered “modest to negligible”; Weights between 0.5-1.0 are considered “substantial”; Weights between 1-2 are considered “heavy”; Weights > 2 are considered “crushing”. For a review, see Gallistel (2009).

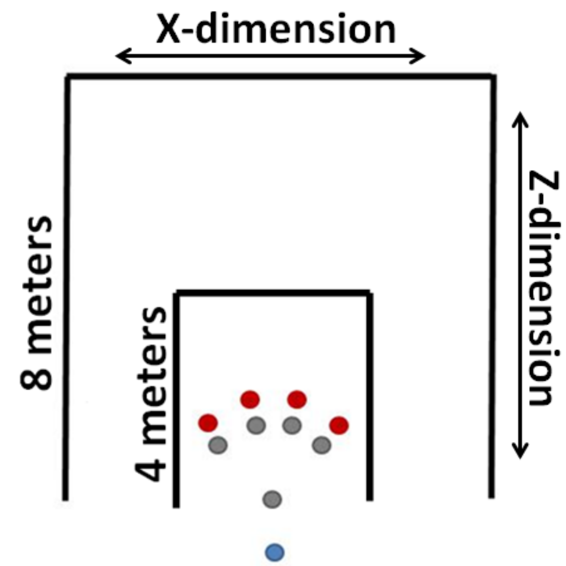

Figure 1. Small and large room condition dimensions. The blue dot indicates the location of the start post. The four red dots indicate possible target post locations for each trial.

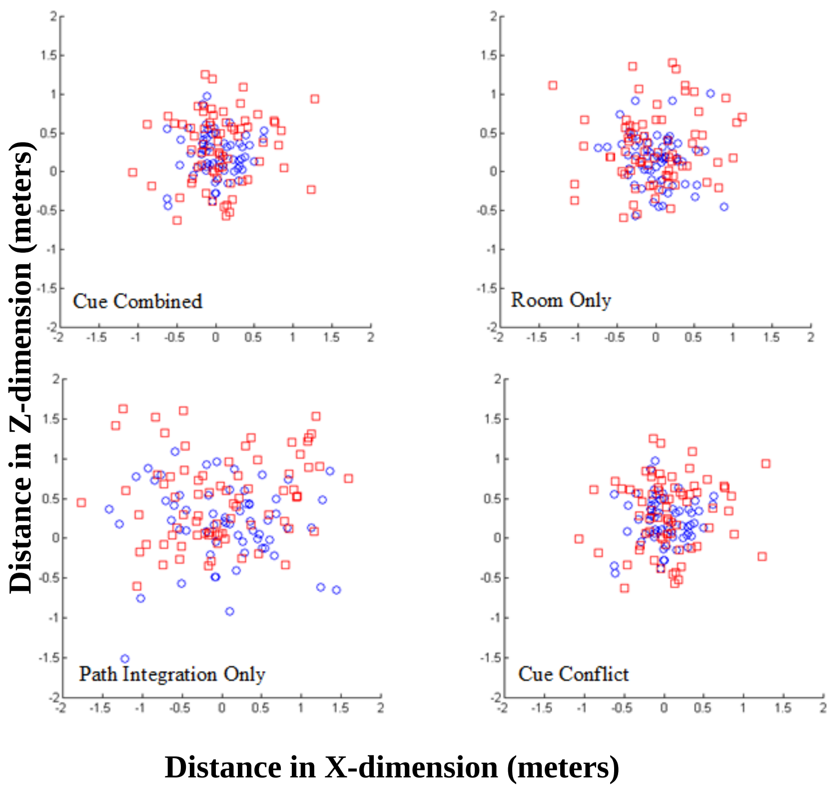

Figure 2. Scatter plots of raw participant responses in each of the four response conditions. Blue circles are small room responses, red squares are large room responses. The actual target location based on path integration is (0,0). The X-axes indicate distance from the target location in the x-dimension in meters. The Y-axes indicate distance from the target location in the z-dimension in meters.

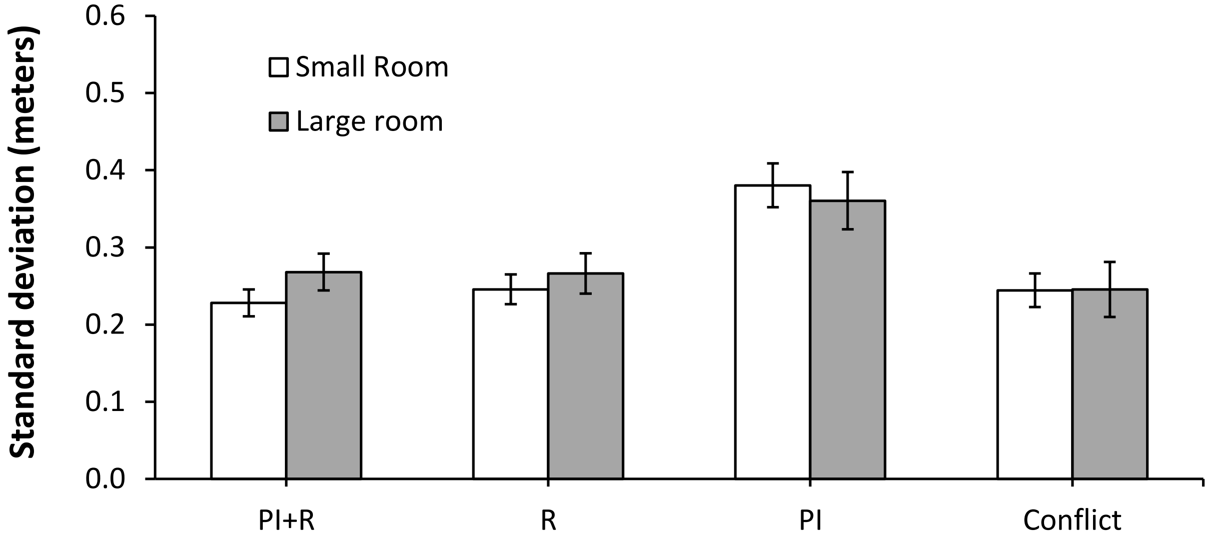

Figure 3. Average response standard deviations as a function of condition and room size in the pilot experiment. Error bars represent +/- 1 standard error. PI+R = combined cue condition, R = room only, and PI = path integration only.

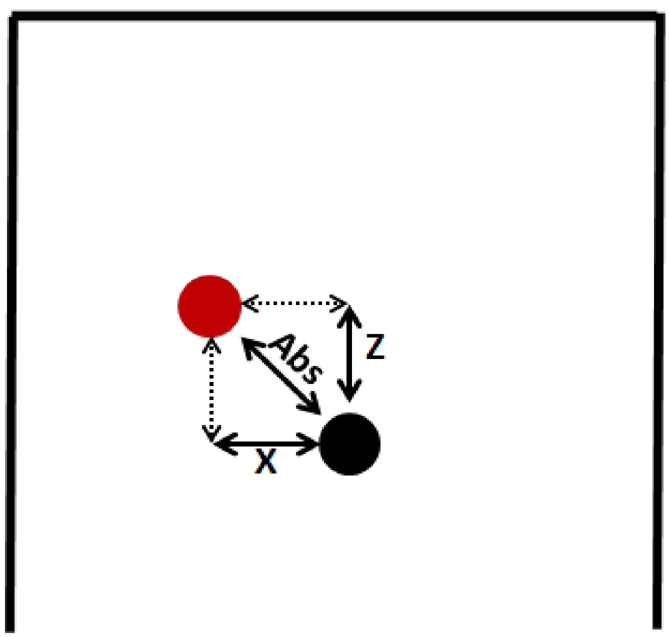

Figure 4. Distance calculated for absolute distances (Abs), Z-dimension distances (Z) and X-dimension distances (X). The red post indicates the correct target location. The black post indicates the participant response location.

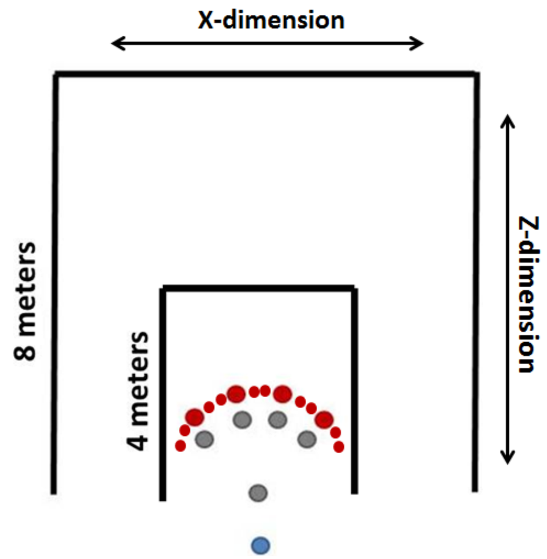

Figure 5. Room sizes and post locations used in Experiment 1. Larger red posts indicate original post locations from the pilot study. All target posts were of identical size during experiment.

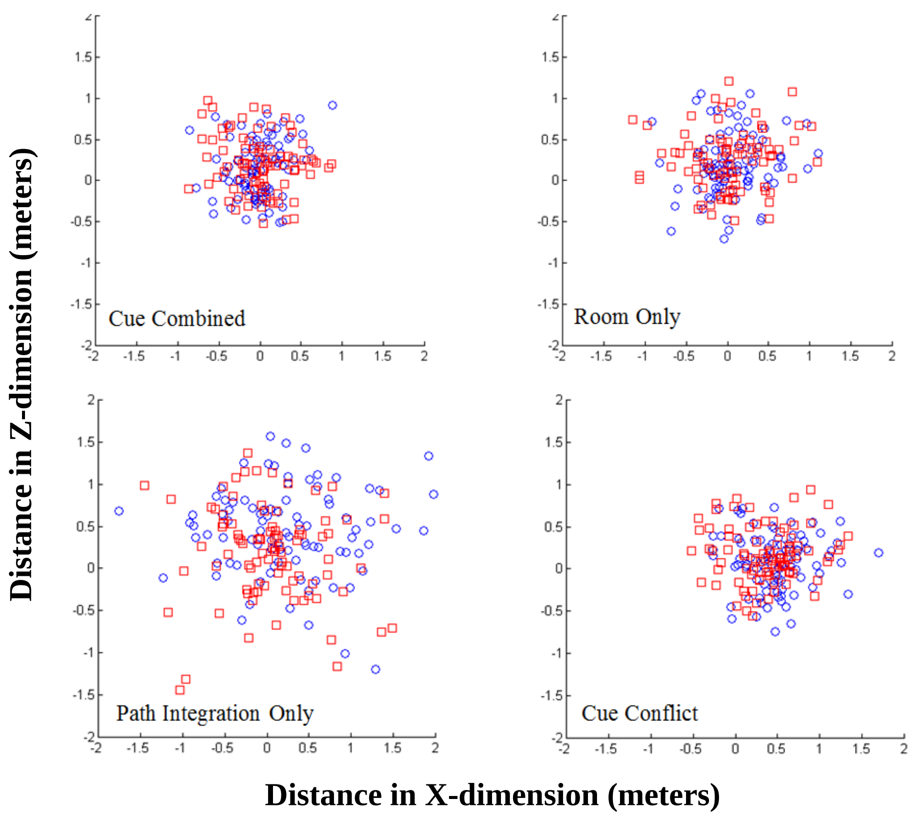

Figure 6. Scatter plots of raw participant responses in each of the four response conditions. Blue circles are small room responses, red squares are large room responses. The actual target location based on path integration is (0,0). The X-axes indicate distance from the target location in the x-dimension in meters. The Y-axes indicate distance from the target location in the z-dimension in meters.

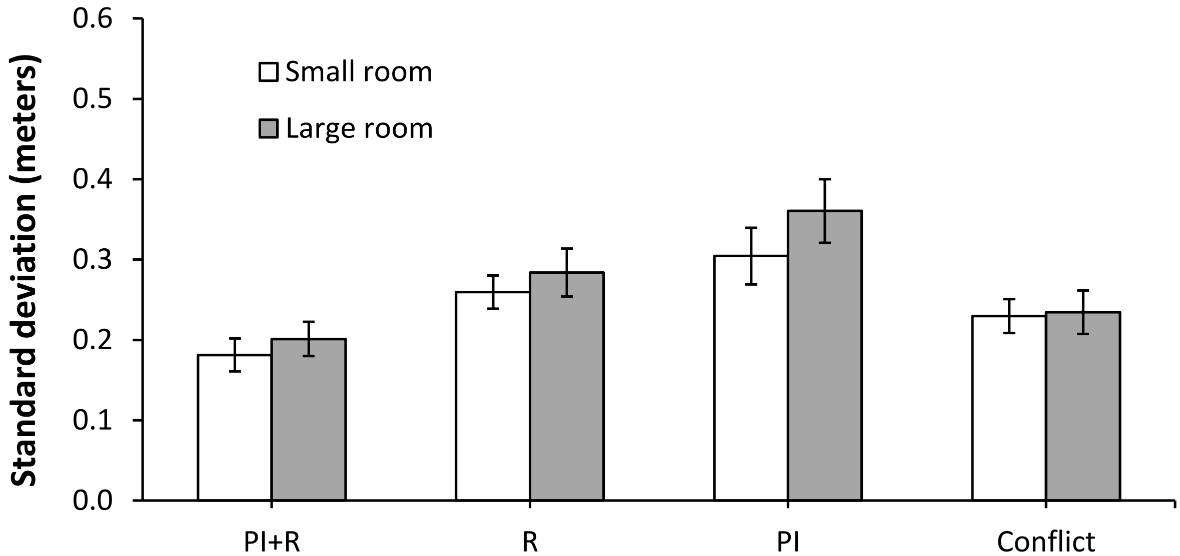

Figure 7. Average response standard deviations as a function of condition and room size in Experiment 1. Error bars represent +/- 1 standard error.

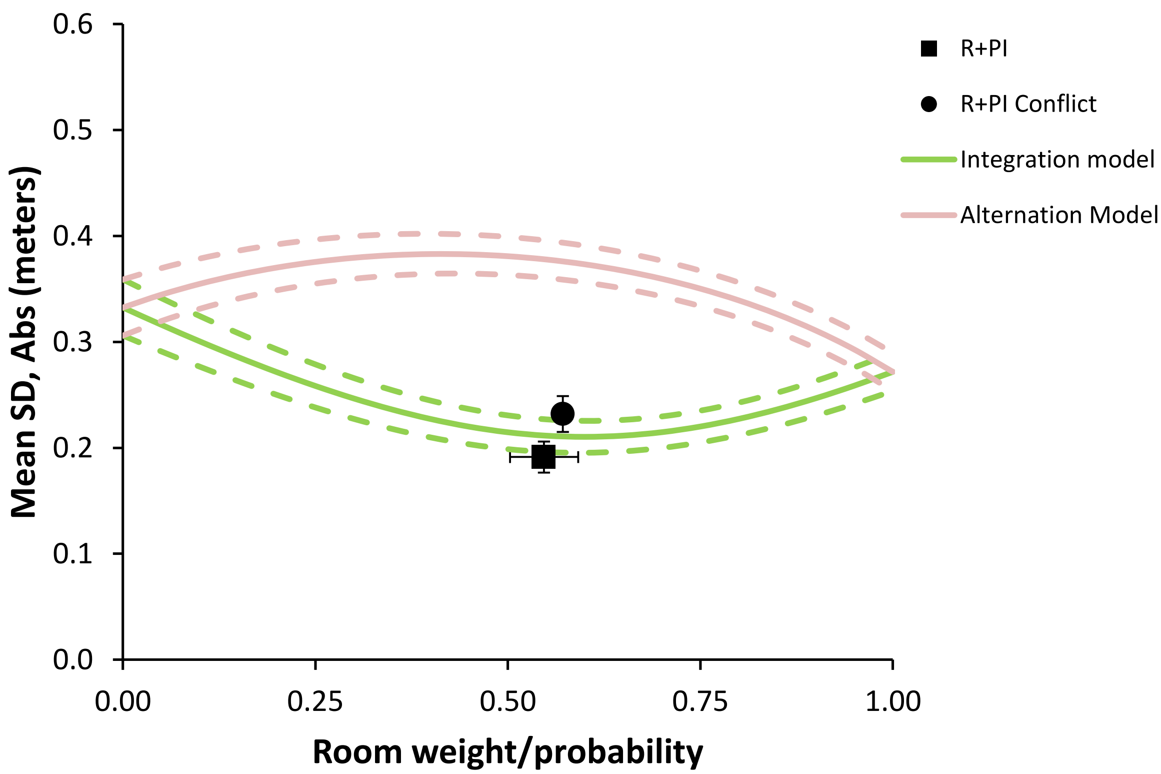

Figure 8. Integration model predicted optimal standard deviation of responses across possible actual room weights and alternation model predicted standard deviation of responses across possible cue use probabilities. The point indicating average actual weight and standard deviation of conflict condition responses is plotted. The point indicating average optimal weight and standard deviation of the combined condition is also plotted. Error bars represent +/- 1 standard error.

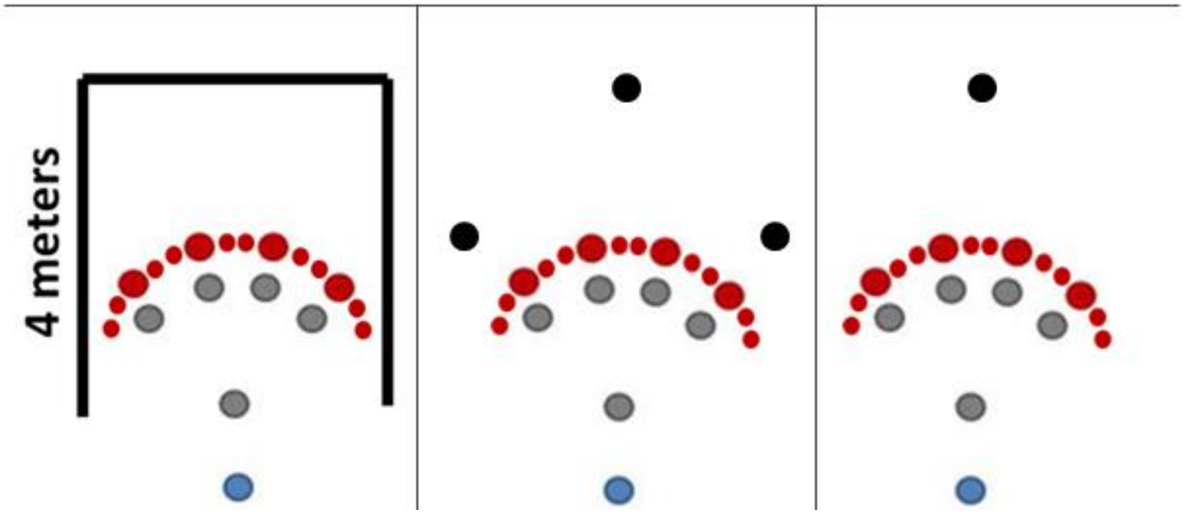

Figure 9. Environmental cue and post locations used in Experiment 2. Larger red circles indicate original post locations from the pilot study. All target posts were of identical size during experiment. Black lines indicate room wall locations in the room condition(left), black circles indicate cue post locations in the multiple landmark (middle) and single landmark (right) conditions.

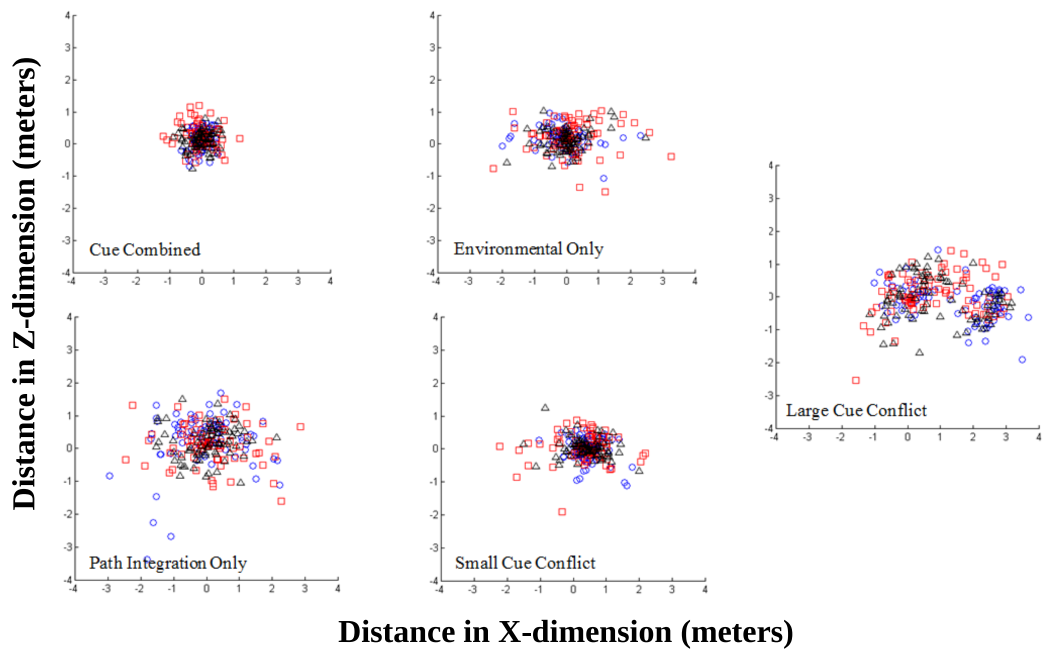

Figure 10. Scatter plots of raw participant responses in each of the five response conditions. Blue circles are room responses, red squares are single landmark responses, black triangles are multiple landmark responses. The actual target location based on path integration is (0,0). The X-axes indicate distance from the target location in the x-dimension in meters. The Y-axes indicate distance from the target location in the z-dimension in meters.

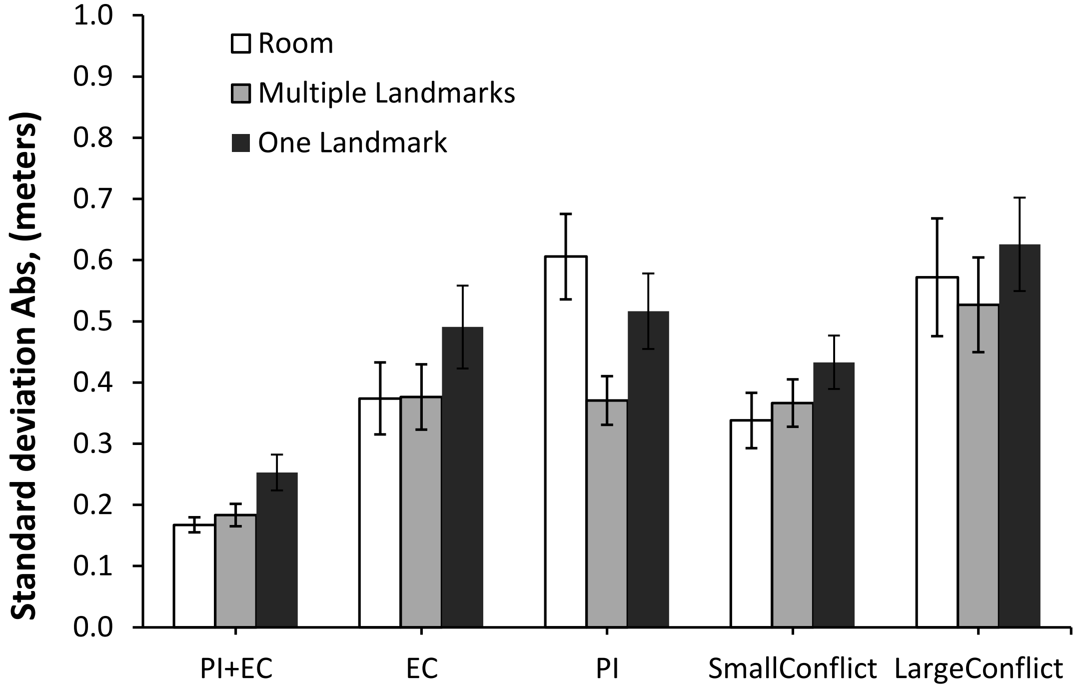

Figure 11. Average response standard deviations as a function of condition and environmental cue weight in Experiment 2. Error bars represent +/- 1 standard error. PI+EC = combined cue condition, EC = environmental cue only, and PI = path integration only

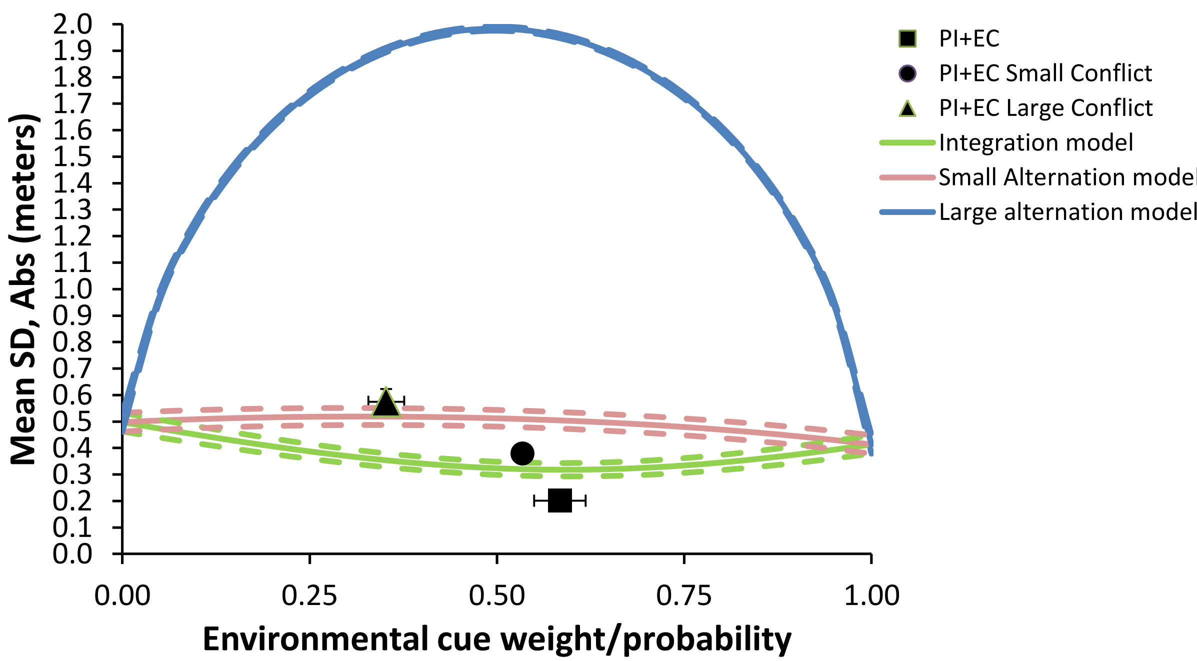

Figure 12. Model predicted optimal standard deviation of responses across possible actual cue weights (integration model) or probabilities of following each cue (alternation models). The points indicating average actual weights and standard deviations of conflict condition responses are plotted. The point indicating average optimal weight and standard deviation of the combined condition is plotted.

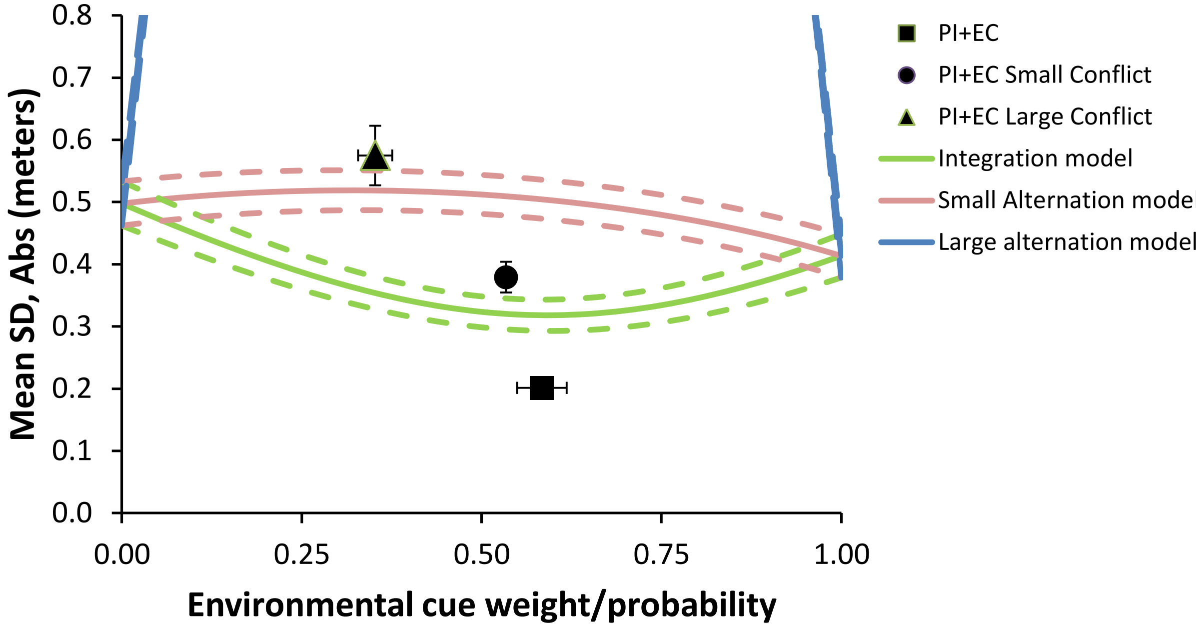

Figure 13. Model predicted optimal standard deviation of responses across possible actual cue weights (integration model) or probabilities of following each cue (alternation models), y-value scale is altered to better represent the integration and small conflict alternation models.