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Bayesian integration of spatial navigation cues

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ABSTRACT

Humans and non-human animals must navigate their environments to survive. A recent question of interest is whether humans have the ability to combine multiple cues to navigation in a Bayesian optimal manner. The current experiments build on previous research examining the combination of cues in adult humans. These experiments further the theoretical understanding of cue combination as well as its application to real-world tasks. Experiment 1 determined that idiothetic path integration cues are not necessary for the optimal combination of path integration and piloting cues. Instead, optic flow, an allothetic path integration cue, was sufficient for the optimal combination of path integration and a geometric cue to navigation. Experiment 2 examined cue combination for two piloting cues to navigation, rather than for a piloting and path integration cue, and found that two piloting cues to navigation are not always combined in a Bayesian optimal manner. Finally, Bayesian cue combination was examined in a two-dimensional desktop environment to determine whether optimal cue integration occurs in the desktop and webpage environments we interact with on a daily basis. Results indicate further study is needed, but illustrate the importance of testing a variety of stimuli when examining cue integration. Together, the following experiments expand the current knowledge regarding how multiple cues to navigation are used together to improve spatial memory and illustrate that small differences in stimuli may have a great impact on the ability to detect optimal cue integration.

CHAPTER 1. INTRODUCTION

Humans and non-human animals must navigate their environments to survive. When you attempt to navigate from your home to your office, you must identify your current location, your goal location, and the desired path between them. Similarly, an ant searching for food must remember the route it has traversed in order to successfully return when the search is complete. When making these navigational judgments, there are an abundance of idiothetic (internal to the navigator) and allothetic (external to the navigator) cues available. A recent question of interest is whether humans have the ability to use multiple cues to assist in reaching their navigational goals and, if so, whether multiple cues are combined in a Bayesian optimal manner. The proposed experiments will build on previous research examining the combination of cues in adult humans. These experiments will further the theoretical understanding of cue combination as well as its application to real-world tasks.

Primary cues to navigation include piloting cues and path integration cues. Piloting occurs when a navigator performs position-based navigation using external signals to their current location (Loomis, Klatzky, Golledge, & Philbeck, 1999). For example, students on the Iowa State campus could find the Memorial Union (MU) building by monitoring their position relative to the Campanile, which is near the MU and visible from many locations on campus. In this example, the Campanile is being used as a piloting cue to navigation. Behavioral and neuropsychological research supports a distinction between two cognitive processes for navigating and reorienting within an environment using piloting cues (see Lee & Spelke, 2010, for review). While the specific distinctions between these two systems would benefit from further study

(Cheng et al., 2013), there is evidence that they rely on different environmental properties, referred to as geometric and landmark cues, and work together while using different computational and brain systems (Lee & Spelke, 2010).

Geometric and landmark cues are allothetic cues to navigation and their use for navigation is referred to as piloting. Geometric cues include objects that are defined by principles of geometry, such as the intersections of streets or the walls in a room. Thus, the shape of the room in which you are currently sitting is a geometric cue because it can be defined solely by extended surfaces and intersections between surfaces. Landmark cues cannot be described solely by the geometry of extended surfaces. Landmark cues are typically more localized than geometric cues and include objects such as a distinctive tree on campus, a colored panel on the wall, or a chair in a room.

Body-based information may also be used as a cue to navigation, and this is referred to as path integration. Path integration is the process of combining allothetic and idiothetic self-motion cues to determine body translation and rotation over time (Loomis et al., 1999). For instance, waking up in the night and walking from bed toward the light switch relies on path integration to know how far one has traveled before reaching the switch. It involves multiple body-based components such as optic flow, vestibular and proprioceptive stimulation, efferent motor commands, and acoustic flow (Loomis et al., 1999). Path integration accumulates error over time and with movement, such that more walking and turning reduces the reliability of path integration as a cue to navigation (Klatzky et al., 1990).

When multiple cue types are available for navigation, it has been found that some types may be relied upon more than others. Previous research has examined the use of geometric and landmark cues when the cues are learned together but are later placed in conflict (i.e., two cues, such as the shape of the room and a colored wall panel, are moved relative to each other to indicate two different target locations). In one forced-choice experiment, rats were found to be highly sensitive to the shape of their enclosure, a geometric cue, but often failed to incorporate the location of a colored wall, a disambiguating landmark, when navigating to a goal location (Cheng, 1986). In addition, rats preferred geometric over landmark cues when the cue-indicated correct locations were placed in a conflict.

In a similar line of experiments using humans, it has been found that geometric cues are often, but not always, preferred over landmark cues during navigation. Ratliff and Newcombe (2008) examined adult humans' relative preference for geometric and landmark cues in navigation using the adaptive-combination model of cue use. The adaptive-combination model (Newcombe & Huttenlocher, 2006) states that preference for a landmark or a geometric cue will be determined by the relative weight associated with each cue. These weights are influenced by several factors, including cue reliability, validity, salience, and previous experience with the cue.

In a test of the adaptive combination model, Ratliff and Newcombe (2008) evaluated relative reliance on room shape and a landmark using a cue-conflict paradigm. Participants learned the location of a hidden object within a rectangular room (a geometric cue) that also contained a colored panel on one wall (a landmark cue). After learning the target location, participants were removed from the environment and the colored panel was shifted so that the correct target location indicated by the panel was in conflict with the correct target location indicated by the shape of the room. Participants were then brought back into the room and asked to indicate the first location they would search for the hidden object. The experimenters manipulated room size, which was expected to influence both the salience of the room (room shape is more salient in a small room because the walls are very close to the navigator and thus more noticeable) and the reliability or usefulness of the room as a cue to navigation (it is easier to return to an unmarked location within a small bedroom than a large airplane hangar because the walls and corners are closer to the target location). It was therefore predicted that the room shape would receive lower weight relative to the colored panel (i.e., the landmark) in the large compared to the small room conditions. It was found that the room-indicated correct location was preferred in a small room while the landmark-indicated correct location was preferred in a large room. This supports the adaptive-combination model, indicating that the preference for geometric and landmark cues depends on the weight assigned to each cue.

Geometric and landmark cues have been examined in relation to each other, and also in relation to path integration cues (external and internal cues that are integrated over time based on body movement). Animal studies indicate that environmental cues, such as landmarks, are relied upon over path integration cues when the cues are placed in a small conflict (e.g., 45 degrees or less) (Chittka & Geiger, 1995; Kohler & Wehner, 2005; Wehner, Michel, & Antonsen, 1996; Whishaw & Tomie, 1997). However, in cases of large conflict (e.g., 180 degrees) between cue-indicated correct locations, environmental cues may be abandoned in favor of path integration cues (Chittka & Geiger, 1995; Shettleworth & Sutton, 2005; Wehner, Boyer, Loertscher, Sommer, & Menzi, 2006; Wehner, 2003). These findings led some researchers to conclude that path integration may function as a backup system for navigation when environmental cues, such as geometric and landmark cues, become unreliable or ambiguous (see Cheng et al., 2007, for review; but also see Zhao & Warren, 2015a). However, path integration may also be used in conjunction with geometric and landmark cues to improve navigation performance when multiple cues are available.

Room shape, a geometric cue, and path integration can be used in combination when remembering a target location within the environment. Kelly, McNamara, Bodenheimer, Carr, and Rieser (2008) demonstrated that room shape and path integration are used together to disambiguate a goal location. Participants navigated in a virtual environment viewed on a head-mounted display (HMD) and performed a spatial updating task to return to the origin of paths of varying lengths. This task was performed within rooms that differed in rotational symmetry and included a circular and a square room. Circular rooms with no identifying features are uninformative as a geometric cue to navigation, as all viewing directions appear identical to the observer. A square room, in contrast, contains more useful information for navigation but is still ambiguous to a completely disoriented participant. If completely disoriented, a participant would only have a 25% chance of indicating a correct target location within a square room. As expected, Kelly et al. (2008) found an increase in spatial updating errors in the circular room with increased path length, consistent with the accumulation of error in path integration over time and movement (Klatzky et al., 1990). However, performance in the square room was unaffected by the length of the travelled path. Given that a completely disoriented participant would select the correct location only 25% of the time in a square room, this indicates participants were able to remain oriented using the noisy path integration cues and the ambiguous room-shape cue in combination. The authors concluded that participants were capable of using path integration and room shape together when navigating in an environment; however, it is unclear how participants were combining information from the cues. It is possible that participants relied on the path integration cue as the primary cue to navigation, while occasionally using the shape of the room to zero-out accumulating path integration error. In contrast, it is also possible that participants were continuously updating their location using path integration and room shape in unison.

One way in which the combination of cues has been examined is through the application of Bayesian principles (Bates & Wolbers, 2014; Butler, Smith, Campos, & Bulthoff, 2010; Cheng, Shettleworth, Huttenlocher, & Rieser, 2007; Knill & Pouget, 2004; Nardini, Jones, Bedford, & Braddick, 2008; Zhao & Warren, 2015b). Bayes' (1763) theorem has been used to determine the optimal way in which multiple cues may be combined to reduce variability in responses when returning to a previously experienced target location. When provided with multiple cues, both of which could be used to determine a target location, the optimal weighting of the two cues is a weighted average in which the weights associated with each cue are inversely proportional to the variability associated with that cue. The cue that produces less response variability when returning to a target location, and is therefore more reliable, should receive a greater weighting than a cue that produces more response variability. For instance, a navigator who walks an outbound path before attempting to return to the origin of the path can use an environmental cue, such as the shape of the room or a landmark within the room, as well as path integration to return successfully. If the path integration cue alone would result in greater response variability when returning to the origin than would the environmental cue alone, then path integration should receive a proportionally lower weight than the environmental cue. Importantly, the optimal solution involves combination of the two cues, rather than reliance on only the most reliable cue. According to Bayes' (1763) theorem, the optimal weights (*W*) associated with two cues (*X* and *Y*) may be determined using the following formulas:

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

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

To calculate the optimal weight associated with each cue, determination of the variability associated with each cue in isolation is necessary. This requires testing participants under single-cue conditions. In the previous example using an environmental cue and path integration, this would entail recording response locations over a number of trials with each cue alone and calculating the variability associated with each.

After calculating the variability associated with each cue and the optimal weights, the actual weight associated with each cue must be calculated for comparison. This determination of actual cue weights requires testing response location in a cue conflict condition (Nardini et al., 2008). In the previous navigation example, this would entail moving one or both of the cues by a sub-threshold amount before the navigator attempts a return path. This conflict, while not noticed by the navigator, places the correct target location based on one cue in conflict with the correct target location based on the second cue. When the navigator attempts to return to the target location, the actual weighting of the cues is indicated by the relative proximity of the responses to each of the conflicting cue-defined correct locations. This relative proximity is given 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. The calculated *rprox* value is used to determine the actual weightings associated with two conflicting cues. An *rprox* value greater than 0.5 indicates that the cue *x* receives relatively greater weight than the cue *y* when the two cues are placed in conflict.

When multiple cues are available at the time of the return path, response variability may be reduced compared to single-cue conditions. When the cue weightings are optimal (see Equations 1 and 2) and both cues are present, then the response variance is predicted by the variability associated with each cue alone. This relationship is 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 variance in either 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 the navigator does not integrate cues and instead alternates between reliance on each cue when the cues are placed in conflict, the variance in their responses may also be predicted (Nardini et al., 2008), as given by:

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

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 greater response variability in a cue conflict condition when compared to single-cue conditions because of the separation between cue-indicated target locations. Interpreting relative proximity, as calculated over multiple trials, as probability of following each cue, we can determine whether actual variability in responses differs from the variability predicted by the model.

In summary, there are four experimental conditions required to determine the optimality with which people combine two cues to navigation: two single-cue conditions, a combined cue condition, and a conflict condition. The first two conditions measure the variability associated with each cue in isolation. These variabilities are used in Equations 1 and 2 to determine the optimal weighting of the two cues. The single-cue variabilities are also used in Equations 4 and 5 to predict variability when two cues are optimally combined or alternated between when both cues are available. The third required experimental condition is both cues in combination. The combined condition provides a measure of actual variability in the combined condition that can be compared to the predicted optimal variability calculated in Equation 4 (using the single-cue variabilities). Finally, the fourth experimental condition is a conflict condition that places the correct target location predicted by one cue in conflict with the correct target location predicted by the other cue. Using Equation 3, the relative proximity of participant responses in the cue conflict condition is used to determine actual cue weightings. These actual cue weightings are compared to the predicted optimal weightings calculated using Equations 1 and 2. Using these four experimental conditions (two single-cue conditions, combined condition, and conflict condition), it can be determined whether participants are combining two cues to navigation in a Bayesian optimal manner.

Nardini et al. (2008) evaluated landmark and path integration cue use among children and adults. The researchers compared spatial updating performance when returning to a target location to predictions of the Bayesian integration model and the alternation model. Adults and children navigated a circular enclosure with 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 all three objects to the location where they retrieved the first object. Path integration and landmark cues were both available on the outbound path, regardless of experimental condition, and experimental manipulations at response created single-cue conditions (path integration or landmark only) as well as two dual-cue conditions (both cues available and cues at a 15° conflict) 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 path integration only condition, the landmarks were hidden from view so that participants only had path integration information available when returning to the first object location. In the landmark only condition, participants were disoriented (the experimenter repeatedly spun them around in a chair) prior to their return path, making path integration useless and causing participants to rely on landmark cues alone for the return path. 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 a 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 throughout the experiment, to allow for response variance to be measured across repeated trials. Integration of the landmark and path integration cues should be reflected by lower variability 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 location 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 variability in responses for adults in the combined conditions relative to single-cue conditions; however, this reduction in variability 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 a Bayesian optimal manner while children appear to alternate between cues instead of combining them.

The results of Nardini et al. (2008) indicate that adult humans appear to optimally combine landmark and path integration information when navigating in the environment. Additionally, previous research (Kelly et al., 2008) indicates that adults use both geometry and path integration to improve memory performance when navigating. Sjolund (2014) adapted the methods of Nardini et al. (2008) to examine the optimality of integration between room shape (a geometric cue) and path integration.

Sjolund (2014) provided participants with two cues to navigation in an immersive virtual reality environment: a virtual 3-walled room and path integration. The use of an immersive virtual environment allowed participants to physically walk and turn through space as they navigated; thereby providing path integration cues to navigation (see Loomis et al., 1999). 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 vertical post (blue circle in Figure 1), facing into the virtual room. At the start of a trial, a red target post appeared at one of fourteen possible target 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 (provided by the virtual reality system) indicated they had reached the location of the target post, the post disappeared and a gray post appeared at one of two possible 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 by increments of three (provided verbally by the experimenter; e.g., "Count backwards by 3 starting at 158").

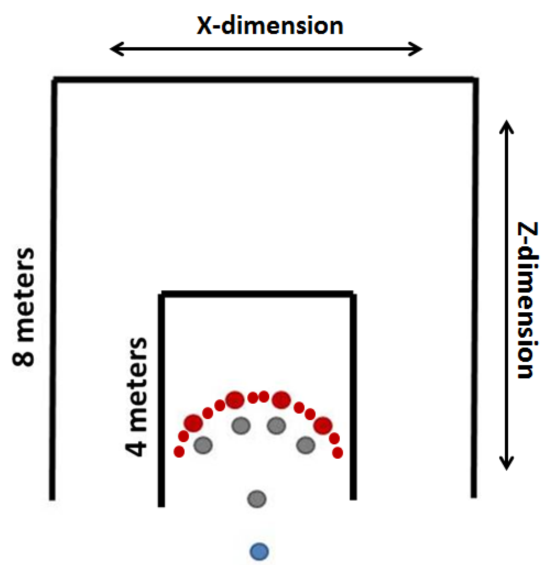


Figure 1. Room sizes and post locations used Sjolund (2014). Larger red dots indicate original post locations from Nardini et al. (2008). All target posts were of identical size during the experiment.

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 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 immersive virtual reality system. In the cue combined condition, participants were able to use both the room shape and path integration cues to attempt to return to the location of the target post (i.e., the virtual ground plane and room appeared, and participants were not disoriented). 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, which were later used to calculate response variability under the different conditions.

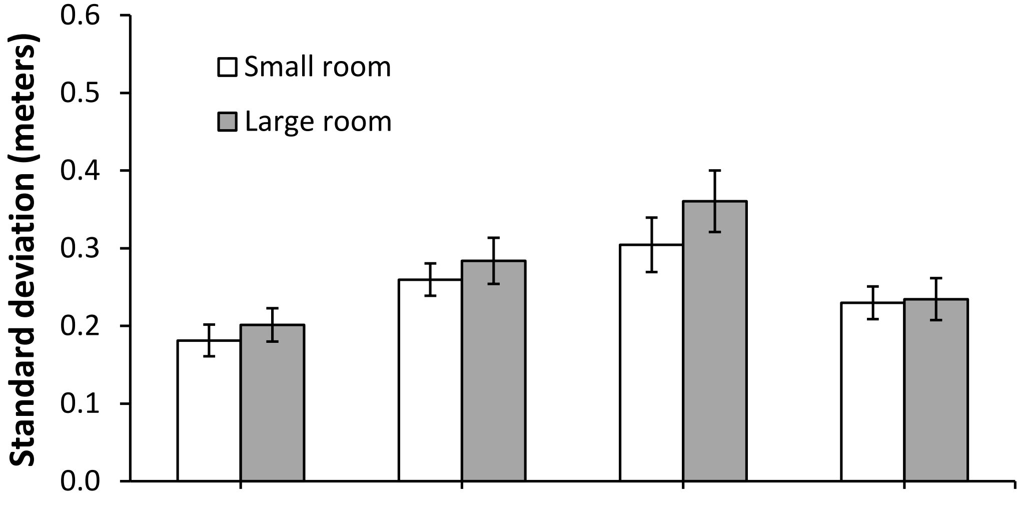


Figure 2. Average response standard deviations as a function of condition and room size in a Sjolund (2014). Error bars represent +/- 1 standard error.

Sjolund (2014) found that response variability when returning to the path origin, measured as standard deviation, was reduced when both cues were available compared to single-cue conditions (see Figure 2). Additionally, responses on cue conflict trials reflected the optimal weightings predicted by the single-cue conditions (see Figure 3 and Table 1). These findings suggest that humans integrate room shape (a geometric cue) and path integration during navigation in a Bayesian optimal manner.

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 Sjolund (2014). *P*-values from standard null hypothesis testing using paired-samples *t*-tests are included.

Experiment	Comparison	Odds in favor of the null	Weight	*P*-value
Sjolund (2014)	Optimal/Actual Weight	8.4:1	-0.92	.54
	Actual/Pred. SD Conflict	8.3:1	-0.92	.66

Note. Odds <3:1 are considered "weak"; Odds between 3 and 10:1 are considered "substantial"; Odds between 10 and 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 and 1.0 are considered "substantial"; Weights between1 and 2 are considered "heavy"; Weights >2 are considered "crushing". For a review, see Gallistel (2009).

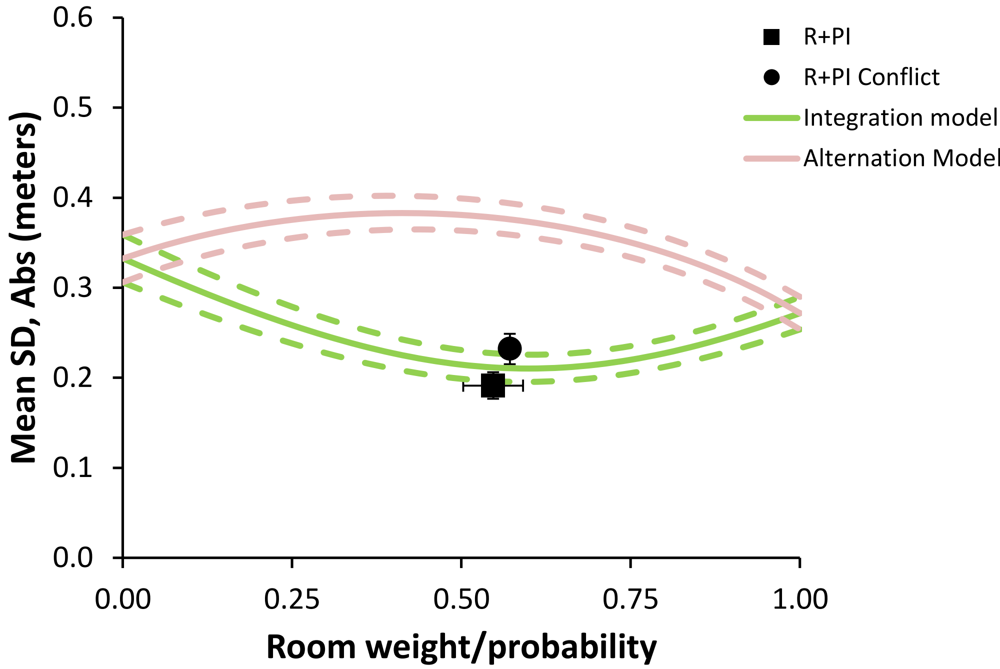


Figure 3. Integration model predicted optimal standard deviation of responses across possible actual room weights and alternation model predicted standard deviation of responses across possible cue use probabilities from Sjolund (2014). The point indicating average actual weight and standard deviation 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.

Results of Nardini et al. (2008) and Sjolund (2014) indicate that humans optimally combine landmark and room-shape cues with path integration cues when navigating an environment. However, path integration involves several allothetic and idiothetic cues, and it is unclear to what extent these different cues influence cue integration. Experiment 1 determined whether idiothetic cues are necessary or if allothetic cues are sufficient for optimal combination of path integration with room-shape cues by preventing physical rotation and translation (and the associated idiothetic cues) through the use of a desktop computer display.

Additionally, previous experiments examining the combination of multiple cues to navigation have focused on the combination of piloting cues (landmarks or geometric cues) and path integration (Nardini et al., 2008; Sjolund, 2014; Zhao & Warren, 2015b), with little focus on the combination of multiple piloting cues in the absence of path integration. The second experiment determined whether two piloting cues to navigation are combined in a Bayesian optimal manner to improve performance when returning to a previously visited location.

Experiments 1 and 2 examined the combination of cues to navigation in a three-dimensional virtual desktop environment. However, much of the desktop navigation we experience in real life is in two-dimensional rather than three-dimensional environments, and these two-dimensional environments also have multiple cues that could be used to remember target locations. For instance, when navigating a webpage, the pages are often designed with boxes of text (similar to three-dimensional geometric cues) and buttons or links (similar to landmark cues). It is unclear how these cues may be used in combination to remember target locations in a two-dimensional environment. The third experiment modified the methods used in Experiments 1 and 2 to examine memory for spatial locations in a two-dimensional environment. Previous research and the current experiments have been summarized in Table 2.

Together, the current experiments further progress the state of the research on Bayesian combination of cues to spatial navigation. The results demonstrate that idiothetic path integration cues are not necessary for the optimal combination of path integration with geometric cues, and the allothetic path integration cue of optic flow is sufficient for optimal integration (Experiment 1). Next, the results indicate that landmarks and geometric cues are combined for navigation in the absence of path integration, but that this combination is not consistent with Bayesian predictions

(Experiment 2). From there, the examination of Bayesian combination of cues in a two-dimensional environment attempted to elucidate whether Bayesian integration occurs when navigating virtual displays used on a regular basis, such as computer desktop and webpage environments (Experiment 3), however, it instead illustrated that cue combination depends on the stimuli being examined. The current experiments inform our understanding of adult human navigational capabilities, as well as provide greater understanding of how users interact with desktop and webpage environments.

Table 2
Summary previous research and the current experiments in terms of environment in which cues were displayed and the cue types examined for optimality.

	Environment				**Cues**			
	Real World	HMD	Desktop		Geometric	Landmark	Path Integration	
			3D	2D			All	Optic Flow
Nardini et al. (2008)	X					X	X	
Sjolund (2014)		X			X		X	
Experiment 1			X		X			X
Experiment 2			X		X	X		
Experiment 3				X	X	X		

CHAPTER 2. EXPERIMENT 1

Sjolund (2014) used immersive virtual reality and Nardini et al. (2008) used a real-world environment to examine the combination of visual, allothetic cues with the entirety of available path integration cues to navigation. Path integration consists of allothetic cues such as optic flow and acoustic flow and idiothetic cues such as vestibular and proprioceptive stimulation and efferent motor commands (Loomis et al., 1999).

While it is important to understand the combination of path integration and environmental cues while navigating in real and immersive environments, it also is important to understand their combination in virtual displays in which physical body rotation and translation are not possible, such as when navigating a desktop environment[1]. For instance, when navigating within a desktop environment, as when using a video game or when attempting to navigate a route using Google Maps Street View, optic flow information is available from the screen, but physical translation and rotation are not available with virtual movements.

[1] It is possible to prevent physical translation and rotation using an HMD system by having participants wear the display but move using an input other than physical movement, such as with the use of a joystick or keyboard input device (for example, Kearns, Warren, Duchon, & Tarr, 2002). Given that Sjolund (2014) was conducted using an HMD, an HMD display could also be used in the proposed experiments. However, the extended use of an HMD will result in simulator sickness symptoms in 50% of users (Kennedy, Lane, Berbaum, & Lilienthal, 1993), and is likely tied to conflict between visual and vestibular sensory input (Chance, Gaunet, Beall, & Loomis, 1998). Additionally, the attrition of participants due to simulator sickness may influence experimental results because those who rely more on optic flow will likely experience more adverse symptoms (Kearns et al., 2002). Given that the use of an HMD is not required for the manipulations of interest, and given the increase in visuo-vestibular conflict that will arise from preventing physical movement in an HMD system, it was decided that the benefit of using an HMD system was not worth the likely discomfort to participants and possible changes to results due to attrition.

From an applied perspective, it is important to understand navigation when physical movement is prevented because the use of desktop and console video games has increased dramatically over the last few decades, with between 10 and 15 percent growth annually (Cadin & Guerin, 2006; Zackariasson & Wilson, 2010). To design video games to promote realism and accurate navigation, we must know how similar or dissimilar navigation may be in a video game environment when compared to navigation in a real environment. If optic-flow cues are combined with piloting cues (geometry and landmarks), this would suggest that cue combination occurs similarly in video games and real-world navigation tasks. If, however, optic flow is not combined with piloting cues for navigation, this could inform video game design by suggesting that providing participants with extra piloting cues to assist in virtual navigation will improve navigation performance and, perhaps, overall video game enjoyment.

Understanding the role of optic flow in navigation is also important from a theoretical perspective. There have been several studies examining the ability of adult humans to navigate using body-based and auditory flow path integration cues in the absence of visual path-integration cues (Loomis et al. 1993; Thompson, 1980; 1983). These experiments typically employ a blindfolded walking task, preventing any visual information from being used as a path integration cue. It has been found that participants are generally able to navigate using path integration in the absence of visual cues, but that responses tend to be variable and biased (Fujita, Klatzky, Loomis, & Golledge, 1993). What has been less studied is how well adult humans are able to navigate through the use of optic flow in the absence of body-based cues. The cues relied on for wayfinding when vision is available may be different from the cues relied on when vision is not available

(Fujita et al., 1993), and this may influence the combination of these cues for improving navigation precision.

Some research has suggested that optic flow may not be sufficient for accurate navigation, especially when routes are long, complex, or require rotation (Chance, Gaunet, Beall, & Loomis, 1998; Klatzky, Loomis, Beall, & Golledge, 1998; Rieser, 1989). This has led to the conclusion that humans cannot navigate accurately using only optic flow information without accompanying body movement, especially for body rotations (Rieser, 1989). However, Riecke, van Veen, and Bulthoff (2002) have found that there are no systematic errors in navigation resulting from the use of optic flow alone. They instead found that a large, curved projection screen was adequate for orientation and navigation with no path integration cues provided aside from optic flow. Similarly, Kirschen, Kahana, Sekuler, and Burack (2000) found that optic flow was beneficial to navigation in a virtual desktop environment, allowing participants to remain oriented as they traversed both learned and novel routes lacking in other available cues.

Kearns, Warren, Duchon, and Tarr (2002) noted the lack of research on optic flow as a path integration cue in the absence of body-based (idiothetic) cues. In three experiments, the roles of optic flow and body-based path integration cues were examined using the same task and the same environment. Participants completed a triangulation task that required them to traverse a two-leg outbound path before attempting to return to the path origin. In the first two experiments, participants wore an immersive head-mounted display while moving through the use of a joystick, which provided optic-flow cues without body-based movement cues. In the third experiment, participants were allowed to physically walk instead of using the joystick, thus providing body-based path integration cues. It was found that participants were able to navigate using optic flow in the absence of body-based cues, but that responses were more variable than navigation by body-based cues. Additionally, the pattern of bias shifted from underestimating angles and distances without body-based cues to overestimating angles and distances with body-based cues. Kearns et al. (2002) concluded that adult humans are able to navigate using optic flow alone, but prefer to use body-based cues when they are available, as indicated by the change in bias when body-based cues were provided.

Additional research has indicated that body-based and optic-flow cues may be combined when both cues are available (Butler et al., 2010; Fetsch, Turner, DeAngelis, & Angelaki, 2009). However, similar to Kearns et al. (2002), it has been found that body-based cues are given more weight than optic-flow cues (Campos, Byrne, & Sun, 2010; Butler et al., 2010) even to the point of indicating a suboptimal weighting of the two cues (Butler et al., 2010; Fetsch et al., 2009). Instead, body-based cues often appear to be given more weight than would be predicted to be optimal based on single-cue variability (Butler et al., 2010; Fetsch et al., 2009).

While path integration cues have been examined extensively in isolation, and optic-flow has been studied to determine how it is combined with body-based cues, it is unclear how optic-flow information is combined with environmental cues when there are no available body-based cues. Due to the suboptimal weighting of optic flow compared to body-based cues when both cues are available (Butler et al., 2010; Fetsch et al., 2009), it is possible that optic-flow information alone will not be combined with environmental cues in a statistically optimal fashion. Instead, there may be an overreliance on an environmental cue over optic-flow information when placed in conflict.

Experiment 1 will determine the variability in navigation performance resulting from navigation by optic flow alone as compared to a geometric (room-shape) cue. It will also determine whether adult humans can combine optic flow (an allothetic path integration cue) with a geometric cue in a Bayesian optimal manner, as occurs when idiothetic path integration cues are also available (Sjolund, 2014). Path integration is dominated by idiothetic self-motion cues, such as proprioceptive and vestibular cues, when both idiothetic and allothetic path integration cues are available (Butler et al., 2010; Campos et al., 2010; Fetsch et al., 2009; Kearns et al., 2002). Therefore, it is important to understand the use of allothetic cues to navigation in the absence of the highly-weighted idiothetic cues to navigation. This is especially important given the increased use of optic flow navigation in the ever growing video game industry (Cadin & Guerin, 2006; Zackariasson & Wilson, 2010). Experiment 1 determined whether the optic flow provided through a desktop computer is sufficient for optimal combination with a geometric (room shape) cue to navigation. It was hypothesized that humans would optimally combine optic flow provided from desktop navigation with a geometric cue in order to improve precision when returning to a previously visited target location.

Method: Experiment 1a

Participants

The effect size from the planned contrast comparing the room only condition to the cue combined condition from Sjolund (2014) was used to calculate a priori power for Experiment 1a. A power analysis using the G*power computer program (Faul, Erdfelder, Lang, & Buchner, 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. Due to the differences in the proposed methodology when compared to previous research, a more conservative target sample of 40 participants was obtained.

Forty-one undergraduate students (19 female, 22 male) from Iowa State University participated for course credit. Trial responses were removed if participants responded in the direction opposite of the target direction, likely indicating they had a lapse in attention and did not turn around prior to response. Eighteen individual trials (3% of total trials) were removed for response in the opposite direction and these trials were spread across all four conditions. A trial response was considered outlying if it fell three times the interquartile range above the third quartile of response distances relative to the condition mean (third quartile plus three times IQR). Four trials were removed as outliers (less than 1%) and these trials were spread across all four conditions. Two participants were removed from analyses due to multiple outlying responses that prevented calculation of standard deviation in at least one of the four conditions.

Procedure

The procedure for Experiment 1a was identical to the procedure of Sjolund (2014), with four changes. First, the task was completed on a desktop computer, rather than in immersive virtual reality. An example of the participants' view is shown in Figure 4. The use of a desktop display allows for optic flow from virtual movement, without allowing physical body movement through the environment. This dissociation of allothetic and idiothetic path integration cues will determine whether optic flow is sufficient to produce integration of cues when remembering a previously visited location within the environment.

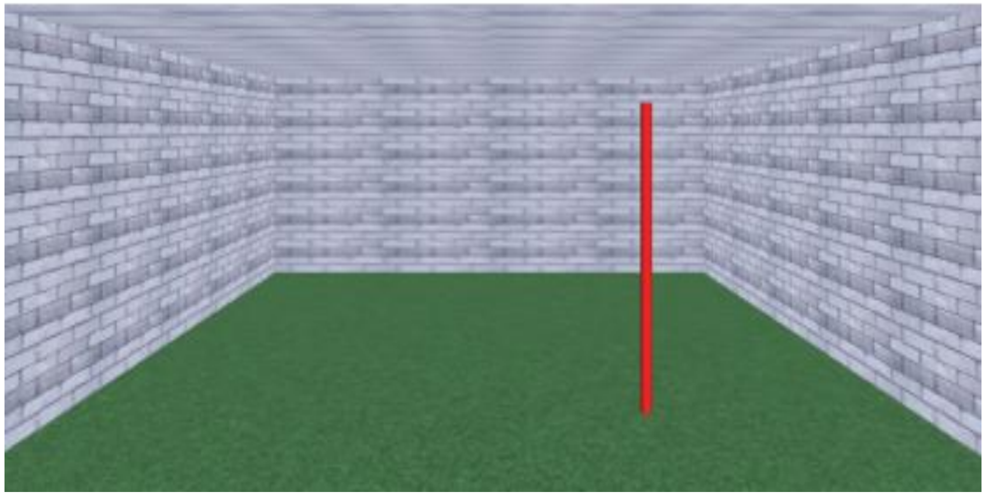


Figure 4. Example view from the start of a trial in Experiment 1a. The red post indicates the target location for this trial.

The second change to the procedure follows from the first change from an immersive virtual environment to a desktop virtual display. On room-only trials, when participants previously were spun in place to disrupt path integration cues, participants instead appeared in a random location in front of the room and at a random orientation. By moving the participants to a random location and orientation, path integration information obtained from optic flow was no longer a useful cue to navigation for returning to the target location (i.e., the target location is no longer 130 degrees and 4 feet away)[2]. The participants were then required to rely on the shape of the room itself to reorient and navigate directly to the location of the previously visited target post.

[2] Path integration is the process of updating one's perceived current location (both position and orientation) over time during self-motion (Loomis et al., 1999). In order to successfully path integrate, the navigator must know his/her previous location and continuously update his/her perceived current location based on sensory inputs. Moving participants to a random location and orientation disrupts the path integration process by disorienting them and requiring them to reorient based on their new location. This prevents participants from using path integration to remember the target post location learned at the beginning of that trial.

Because participants appeared in a random location and orientation, optic flow was no longer a useful cue for returning to the target location and the variability associated with the room cue alone could be determined.

The third change to the procedure is that participants were no longer split into large and small room conditions and, instead, all participants experienced the large room condition (Sjolund, 2014, reported no effect of room size). The large room was used as a geometric cue to navigation because the larger size would allow future experiments to incorporate additional manipulations, such as providing landmarks, without altering the room cue.

The fourth and final change to the procedure was the inclusion of a distant landmark in the direction opposite the virtual 3-walled room before the start of the return path. The distant landmark was included based on feedback from pilot participants that they would sometimes make a full 360 degree rotation in the optic flow only condition before realizing the room was missing on that trial. After a full rotation, the pilot participants lost track of their current orientation. By including a distant landmark opposite the room, participants were able to reset their orientation after a full rotation and then begin their return path with the knowledge that they must rely on path integration alone to navigate to the target location. When the participant moved the virtual equivalent of 0.5m from the start of the return path, the distant landmark disappeared to prevent its use as a cue to the target location.

Aside from the aforementioned changes to the procedure, all stimuli and methods were identical to Sjolund (2014). In summary, Experiment 1 included the four experimental conditions needed to determine whether two cues are combined in a

Bayesian optimal manner. Two single-cue conditions (room only and optic flow only) were included to allow for the calculation of Bayesian optimal cue weights using Equations 1 and 2 and predicted optimal standard deviation using Equation 4. A combined condition (room and optic flow together) provided a measure of actual standard deviation to be compared with the predicted optimal standard deviation that was calculated using Equation 4. Finally, a conflict condition placed the correct target location indicated by the room in conflict with the correct target location indicated by optic flow. The relative proximity of participant responses to each of the two cue-indicated correct locations was used with Equation 3 to determine actual cue weightings. Actual cue weightings were compared with the optimal cue weightings predicted using the single-cue condition variabilities and Equations 1 and 2.

Participants were seated at a desktop computer and began each trial outside of a three-walled virtual room. A red target post appeared at one of fourteen possible target post locations (Figure 1). Participants moved to the target post location using the arrow keys on the computer keyboard. When participants reached the target post location, the target post disappeared and a gray post appeared on the opposite side of the virtual room (Figure 1). After participants navigated to the first gray post, a second gray post appeared at the virtual equivalent of one meter in front of the original start location (see Nardini et al., 2008). When participants reached the location of the second gray post, they turned to face the location of the original blue start post. At this time, the desktop display showed a blank, gray screen for fifteen seconds. During the fifteen second pause, participants were required to complete a subtraction distractor task by entering numbers into the computer. This subtraction task disrupted verbal and visual retrieval strategies prior to response. After fifteen seconds elapsed, the display returned and participants were asked to navigate directly to the location of the previously viewed target post using the keyboard arrow keys. When the participant believed they had reached the target post location, they recorded their response location through a key press.

Analyses: Experiment 1a

Because the target locations were randomly selected from fourteen possible target locations, participants' responses were aligned (rotated and translated) to a single target location prior to analysis. Using the aligned responses, analyses focused on the comparison of the standard deviations of participant responses across four repeated trials per condition around each participant's own mean response location. Systematic bias in responses did not influence the standard deviation of responses. Initial analyses followed those of Nardini et al. (2008) and Sjolund (2014) 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.

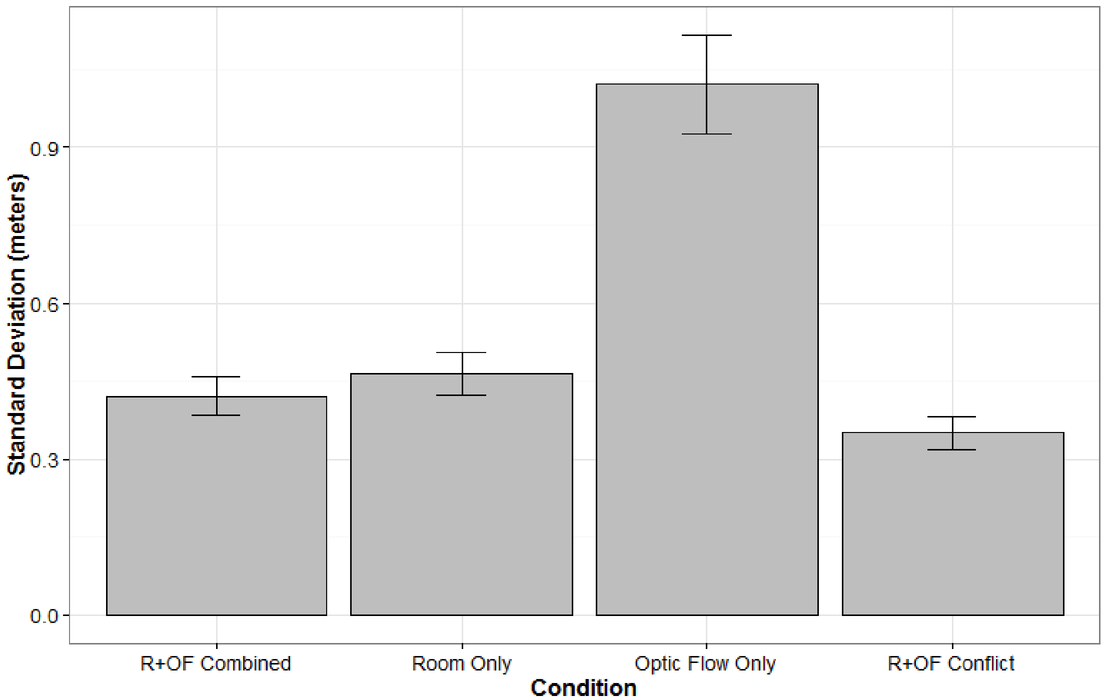
For example, if the target location is located at the (x, z) coordinates (0, 0), a participant attempting to navigate to this location across four separate trials might respond at the coordinates (4, 2), (-6, 3), (-5, -1), and (3, 0). The mean X location would be (4+-6+-5+3)/4 and the mean Z location would be (2+3+-1+0)/4 for a mean response location equal to (-1, 1). The mean response location is then used to calculate the absolute distance of each individual response from the mean. The absolute distance from (4, 2) to (-1, 1) would be calculated as $\sqrt{(4+1)^2 + (2-1)^2} = 5.10$. Similarly, the absolute distance from (-6, 3) is 5.39, from (-5,-1) is 4.47, and from (3, 0) is 4.12. Standard deviation of these absolute distances is then calculated and compared across the experimental conditions to determine response variability. These standard deviations were used to calculate the Bayesian optimal weighting of cues when navigating to the target location (Equations 1 and 2).

Results and Discussion: Experiment 1a

Standard deviations based on absolute response distance (see Figure 5) were analyzed in a one-way ANOVA for response condition (combined, room only, OF only, and conflict). The main effect of condition, with Greenhouse-Geisser correction, was significant, $F(3, 111) = 35.98$, $p < .001$, $\eta^2_G = 0.39$[3]. It was predicted that the 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 ($M = 0.42$, $SD = 0.23$) was not significantly different from the standard deviation in the room only condition ($M = 0.47$, $SD = 0.26$), which was the single-cue condition with less variability $F(1, 37) = 1.02$, $p =.32$, $\eta^2_G = 0.01$. The cue conflict condition ($M = 0.35$, $SD = 0.20$) was significantly less variable than the room only condition $F(1, 37) = 5.88$, $p = .02$, $\eta^2_G = 0.06$. An exploratory paired t-test indicated no significant difference between the average standard deviation of responses in the combined cue condition and the cue conflict condition $t(38) = 1.52$, $p = .14$. Standard deviations of responses in the combined cue condition were not different from those of the most precise single-cue condition (room only), and also not different from the cue

[3] Generalized eta-squared values are reported because they provide a measure of effect size that is easier to compare across research designs and more accurately match Cohen's (1988) guidelines for characterizing effect sizes when applied to repeated measure designs (Bakeman, 2005; Olejnik & Algina, 2003).

conflict condition. The cue conflict condition, in contrast, did have significantly lower response variability than the room only condition. The reduction in variability in the conflict condition suggests that participants may have been combining room shape and



optic flow, but that the effect is too small to detect with our current stimuli and sample size.

It is possible that participants were not combining room shape and optic flow to improve performance in the combined cue condition; however, there is no theoretical reason that participants would combine cues in the conflict condition but not combine cues in the combined cue condition. Instead, it is likely that the discrepancy between the precision of the single-cue conditions (i.e., comparison between the optic-flow only and room-only conditions) is so large that the optimal combination of cues is very similar to the use of room shape alone, making it difficult to detect the effect of cue combination.

Figure 5. Average response distance standard deviations as a function of condition in Experiment 1a. Error bars represent +/- 1 standard error.

Whether optic flow is being completely discarded in the combined cue condition or if it is not influencing the combined condition standard deviation due to a low optimal weighting, the theory would predict that single-cue conditions that have more similar standard deviations should show the greatest combination (see Ernst & Banks, 2002).

Given that participants each have their own single-cue standard deviations that would be used to calculate unique cue weights for that participant, it was hypothesized that participants who had more similar standard deviations in the single-cue conditions would show greater evidence of cue integration in the dual-cue conditions. To test this hypothesis, subjects were split into two groups based on the median difference between the room-only and optic-flow-only conditions. The similar group included participants that had standard deviations in the room only and optic flow only conditions that were closer to equal while the dissimilar group included participants that had standard deviations in the single-cue conditions that were more discrepant. After participants were split based on single-cue condition similarity, planned contrasts compared the standard deviation of the dual-cue conditions to the better of the single-cue conditions (room shape in both groups) to evaluate cue combination.

Standard deviations based on absolute response distance for all subjects (see Figure 6) were analyzed using a 2x4 mixed ANOVA. The interaction between single-cue condition similarity (similar, dissimilar) and response condition (combined, room only, optic flow only, conflict) with Greenhouse-Geisser correction was significant, $F(3,108) = 23.17$, $p < .001$, $\eta^2_G = 0.27$. There was a significant main effect of condition, $F(3,108) = 57.54$, $p < .001$, $\eta^2_G = 0.47$, and a main effect of similarity, $F(1, 36) = 4.20$, $p = .048$, η^2_G

= 0.05, with the dissimilar group (M = 0.64, SD = 0.20) having a higher mean standard deviation than the similar group (M = 0.50, SD = 0.20).

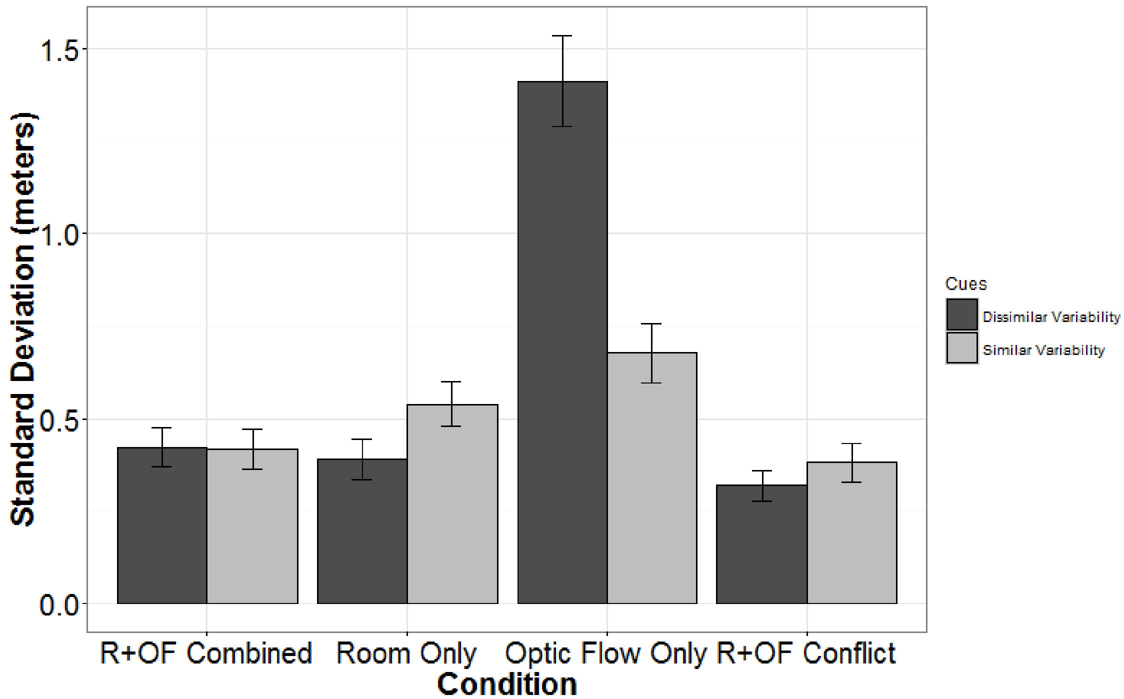


Figure 6. Average response distance standard deviations as a function of condition and single-cue relative variability in Experiment 1a. Error bars represent +/- 1 standard error.

Standard deviations based on absolute response distance (see Figure 6) for the similar group were analyzed in a one-way ANOVA for response condition (combined, room only, OF only, and conflict). The main effect of condition was significant, $F(3, 54) = 7.66$, $p < .001$, $\eta^2_G = 0.16$. The similar group had a significantly lower standard deviation in the combined condition (M = 0.42, SD = 0.23) compared to the room only condition (M = 0.54, SD = 0.26), $F(1, 18) = 5.15$, $p < .05$, $\eta^2_G = 0.06$, as well as a significantly lower standard deviation in the conflict condition (M = 0.38, SD = 0.23) compared to the room only condition $F(1, 18) = 5.14$, $p < .05$, $\eta^2_G = 0.10$.

Standard deviations based on absolute response distance (see Figure 6) for the dissimilar group were also analyzed in a one-way ANOVA for response condition (combined, room only, OF only, and conflict) with Greenhouse-Geisser correction. The main effect of condition was significant, $F(3, 54) = 56.50$, $p < .001$, $\eta^2_G = 0.67$. In contrast to the similar group, the dissimilar group did not show a difference between the combined condition ($M = 0.42$, $SD = 0.23$) and the room only condition ($M = 0.39$, $SD = 0.23$), $F(1, 18) = 0.20$, $p = .66$, $\eta^2_G = 0.004$, or between the conflict condition ($M = 0.32$, $SD = 0.18$) and the room only condition, $F(1, 18) = 1.23$, $p = .28$, $\eta^2_G = 0.03$.

Participants who had more similar standard deviations of responses in the room only and optic flow only conditions also appeared to be combining cues, while those that had less similar standard deviations of responses in the single-cue conditions did not show evidence of cue combination. It is possible that altering the cues to navigation to encourage more similar response standard deviations in the single-cue conditions will result in the combination of cues, as illustrated by increased precision in the dual-cue conditions. Experiment 1b attempted to make the room cue more variable by doubling its size and removing the virtual brick ceiling (which may be used to help participants gauge distance). Aside from the new room size and the removal of the room ceiling (Figure 7), Experiment 1b was identical to Experiment 1a.

Method: Experiment 1b

Participants

Experiment 1a indicated greater variability in the room only condition standard deviation of responses ($M = 0.47$, $SD = 0.26$) compared with Sjolund (2014) ($M = 0.28$, $SD = 0.14$), likely due to the change from HMD to desktop VR. This increase in variability may make it more difficult to detect differences. Therefore, a more conservative sample size of 60 was obtained.

Sixty-two undergraduate students (34 female, 28 male) from Iowa State University participated for course credit. Trial responses were removed if participants responded in the direction opposite of the target direction, likely indicating they had a lapse in attention and did not turn around prior to response. Sixteen individual trials (less than 2% of total trials) were removed for response in the opposite direction and these trials were spread across all four conditions. A trial response was considered outlying if it fell three times the interquartile range above the third quartile of response distances relative to the condition mean (third quartile plus three times IQR). One trial was removed as an outlier (less than 0.2% of all trials) from the conflict condition. One participant was removed from analyses due to the removal of multiple responses that prevented calculation of standard deviation in at least one of the four conditions.

Procedure

The procedure for Experiment 1b was identical to the procedure of Experiment 1a, except for two changes to the room-shape cue (Figure 7). These changes were intended to make the room a less reliable cue to the location of the red target post. The

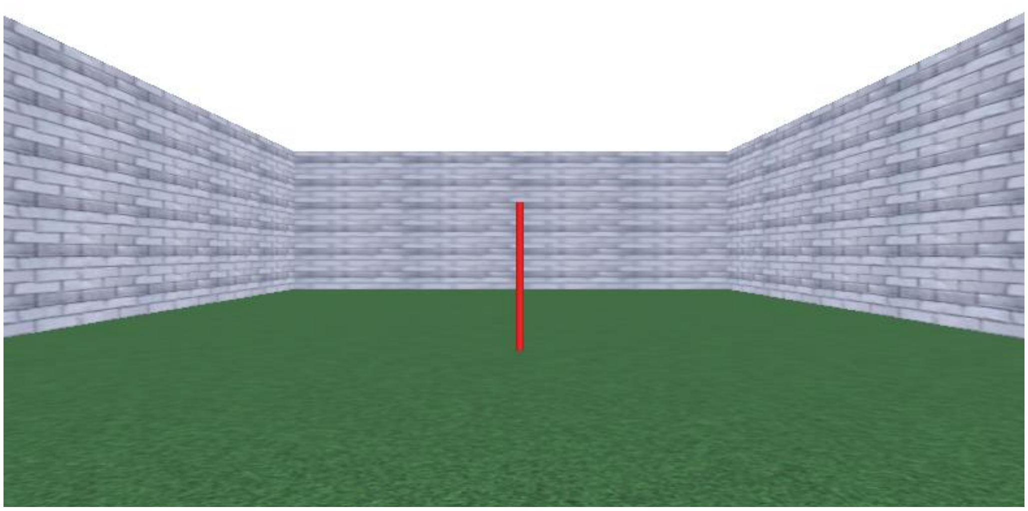
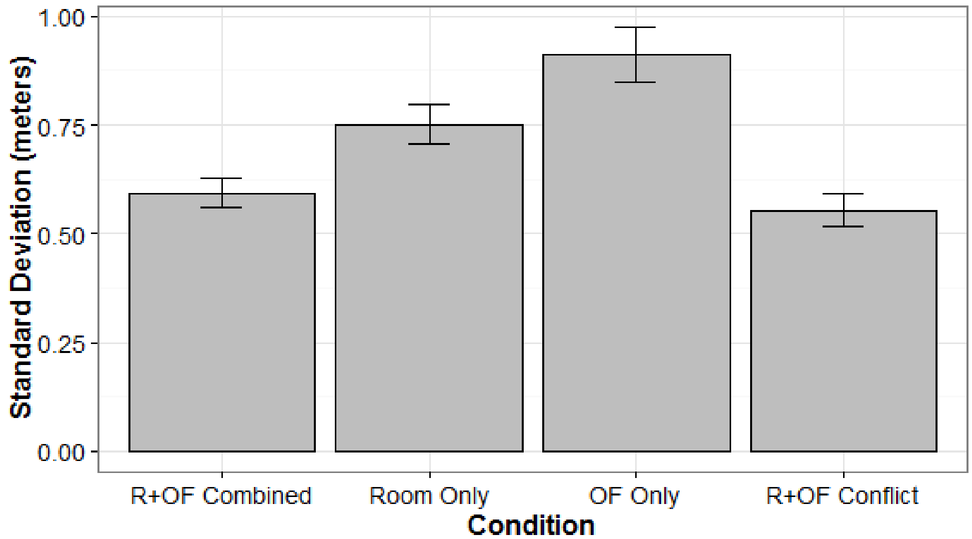


Figure 7. Example view from the start of a trial in Experiment 1b. The red post indicates the target location for this trial.

room was doubled in size to make it more difficult for participants to remember target locations based on their relationships to room walls. Additionally, the roof of the room was hidden so that participants could not use the texture to help them remember the target location.

Results and Discussion: Experiment 1b

Analyses followed those of Nardini et al. (2008), Sjolund (2014), and Experiment 1a. Standard deviations based on absolute response distance (see Figure 8) were analyzed in a one-way ANOVA for response condition (combined, room only, optic flow only, and conflict) with Greenhouse-Geisser correction. The main effect of condition was significant, $F(3, 180) = 12.75$, $p < .001$, $\eta^2_G = 0.14$. To determine which of the two single-cue conditions had the lower response variability, a paired-samples *t*-test compared response standard deviation in the room only condition ($M = 0.75$, $SD = 0.34$) to the response standard deviation in the optic flow only condition ($M = 0.91$, $SD = 0.50$). Response standard deviation in the room only condition was not significantly lower than response standard deviation in the optic flow only condition $t(60) = 1.92$, $p = .06$. It was predicted that the response standard deviation in the cue combined condition would be lower than those in either of the single-cue conditions. Planned contrasts revealed that response standard deviation in the cue combined condition ($M = 0.59$, $SD = 0.26$) was significantly lower than standard deviation in the room only condition, which was the single-cue condition with numerically less variability $F(1, 60) = 9.05$, $p < .01$, $\eta^2_G = 0.06$. The cue conflict condition ($M = 0.55$, $SD = 0.29$) also had significantly lower standard deviation of responses than the room only condition $F(1, 60) = 10.84$, $p < .01$, $\eta^2_G = 0.09$. Response variability was significantly lower in both dual-cue conditions compared to the room only condition, which was the less variable of the two single-cue conditions. This suggests that participants were combining cues to improve navigation precision.



Optimal weights for the room shape and optic flow only conditions were calculated for each participant using the variances from each of the single-cue conditions following Equations 1 and 2. Actual weights for room shape and optic flow were calculated as the relative proximity of responses to the room-defined and optic flow-defined target 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

Figure 8. Average response distance standard deviations as a function of condition in Experiment 1b. Error bars represent +/- 1 standard error.

participant to their actual room shape weight. The optimal weights ($M = 0.55$, $SD = 0.27$) and the actual weights ($M = 0.51$, $SD = 0.03$) were not significantly different $t(60) = 1.01$, $p = .31$, suggesting that participants assigned weights similar to optimal when combining cues. Bayesian analyses indicated odds in favor of the null (JZS prior, scale r on effect size = 0.5 for a small effect) of 3.26:1 (see Rouder, Speckman, Sun, Morey, & Iverson, 2009; Jarosz & Wiley, 2014), which are generally considered “substantial” or “positive” odds (for review, see Gallistel, 2009; Jarosz & Wiley, 2014). This provides support that participant actual cue weights were similar to predicted optimal weights using their single-cue condition variabilities and Equations 1 and 2.

To determine whether there was a significant preference for the room-shape cue or the optic-flow cue in the conflict condition, the relative proximity of responses to the room shape-indicated correct location were 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 greater weight than 0.5, $t(60) = 3.39$, $p < .01$, indicating a significant preference for the room-shape cue over the optic-flow cue in the conflict condition.

Figure 9 illustrates the comparison of 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. Importantly, each individual has his/her own model prediction curve, actual room weight, and standard deviation of responses in the conflict condition. Figure 9 uses the average room weights and standard deviations to display an average of the individual curves. Given the relatively large variability in predicted optimal room weight across participants, the predicted optimal standard deviation illustrated in the figure ($M = 0.62$) is higher than the mean calculated optimal standard deviation ($M = 0.49$).

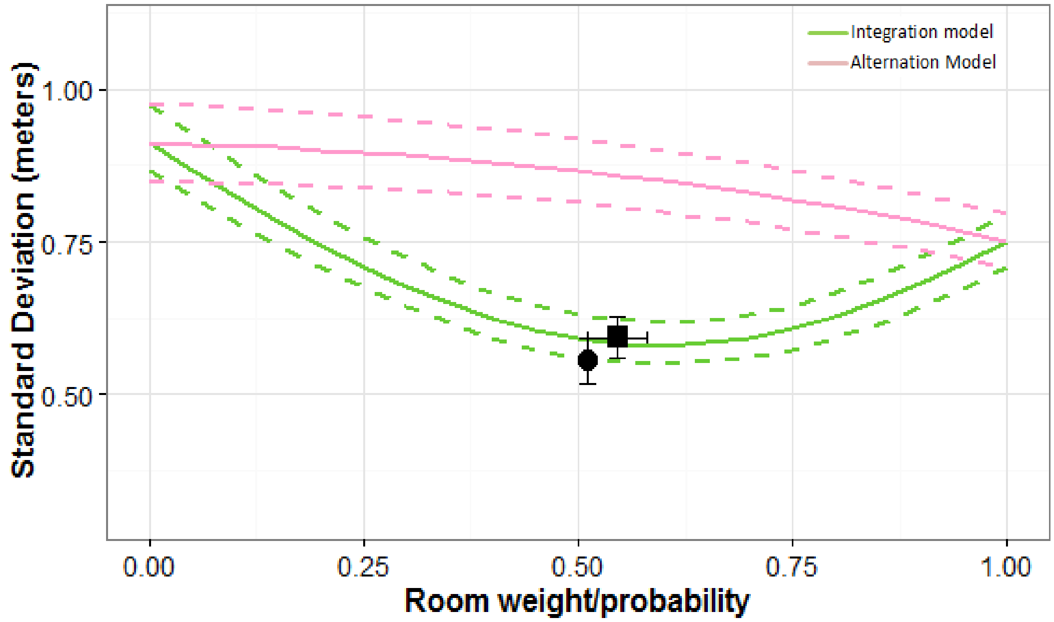


Figure 9. Integration model predicted optimal standard deviation of responses across possible actual room weights and alternation model predicted standard deviation of responses across possible cue use probabilities from Experiment 1b. The point indicating average actual weight and standard deviation of conflict condition responses is plotted (circle). The point indicating average optimal weight and standard deviation of the combined condition is also plotted (square). Error bars represent +/- 1 standard error.

Paired-samples *t*-tests compared each individual's actual standard deviation of responses in the dual-cue conditions to the standard deviation predicted using their calculated optimal cue weights and Equation 4. Participant actual standard deviation of responses in the conflict condition (*M* = 0.55, *SD* = 0.29) were not significantly different from their calculated optimal standard deviation of responses (*M* = 0.49, *SD* = 0.18), *t*(60) = 1.48, *p* = .14, 95% CI [-0.16, 0.02]. While it is often important to make conclusions regarding the similarity of conditions, this is not possible using null hypothesis significance testing (Gallistel, 2009). Instead, Bayesian analyses indicated odds in favor of the null (JZS prior, scale r on effect size = 0.5) of 1.93:1 (Rouder et al., 2009). Participant actual standard deviation of responses in the combined condition (*M* =

0.59, *SD* = 0.26) were significantly higher than their predicted optimal standard deviation of responses (*M* = 0.49, *SD* = 0.18), $t(60) = 2.92$, $p < .01$. The significant difference in the actual and optimal standard deviations in the combined condition may be the result of slight differences in actual and optimal weights (although actual and optimal weights were not found to be significantly different).

A second set of paired-samples *t*-tests compared each individual's actual standard deviation of responses in the dual-cue conditions to the standard deviation predicted using their actual cue weights and Equation 4. This would correct for any differences in standard deviation that resulted from using slightly different actual weights than predicted optimal weights. Participant actual standard deviation of responses in the conflict condition (*M* = 0.55, *SD* = 0.29) were not significantly different from their predicted optimal standard deviation of responses (*M* = 0.62, *SD* = 0.22), $t(60) = 1.34$, $p = .19$, 95% CI [-0.03, 0.16]. Bayesian analyses indicated odds in favor of the null (JZS prior, scale r on effect size = 0.5) of 2.31:1 (Rouder et al., 2009). Participant actual standard deviation of responses in the combined condition (*M* = 0.59, *SD* = 0.26) were not significantly different from their predicted optimal standard deviation of responses (*M* = 0.62, *SD* = 0.22), $t(60) = 0.67$, $p = .50$. Bayesian analyses indicated odds in favor of the null (JZS prior, scale r on effect size = 0.5) of 4.22:1 (Rouder et al., 2009). Given that there was no significant difference between participant actual weights compared to optimal weights and given the general similarity of actual standard deviation compared to optimal standard deviation, it appears participants optimally combined room shape and path integration to improve navigation performance in Experiment 1b.

Discussion

The results of Nardini et al. (2008) and Sjolund (2014) indicated that path integration is combined with environmental cues to navigation in a Bayesian optimal manner when full body movement is allowed. However, there are many instances in which physical body movement is not possible when performing a navigation task. For instance, when navigating a virtual route on a computer screen, either through a video game or a map application, the only available path integration cue is the optic flow provided on the desktop monitor. Additionally, the use of optic flow in the absence of body-based path integration cues has not been studied extensively to determine how optic flow may be used in isolation (Kearns et al., 2002), and optic flow may receive a sub-optimally low weight when combined with body-based path integration cues to navigation (Butler et al., 2010; Fetsch et al., 2009). Experiment 1 sought to determine whether optic flow alone could be used to return to a previously visited target location and, if so, whether optic flow may be optimally combined with room shape to improve navigation precision.

Experiment 1a failed to find sufficient evidence that both optic flow and room-shape cues were used to increase navigation precision in dual-cue conditions. It is believed this was due to a large discrepancy in precision in the single-cue conditions. The room only condition had significantly lower standard deviation of responses than the optic flow only condition. It is possible that this large discrepancy prevented optimal integration of cues. In contrast, optimal integration may have been occurring, but the weight given to the optic-flow cue may have been very small, making it difficult to detect the effect using the sample size of Experiment 1a (n = 41). Exploratory analyses indicated that participants who had more similar response standard deviations in the single-cue conditions also appeared to be using the cues to improve precision in dual-cue conditions. In contrast, the participants who had less similar response standard deviations in the single-cue conditions did not show evidence of using the two cues together to improve precision in the dual-cue conditions. While the current design does not allow us to determine whether the failure to find evidence of integration in Experiment 1a was due to suboptimal integration or due to an especially low optimal weight for optic flow, it was predicted that increasing response variability in the room only condition would encourage more clear integration of cues in Experiment 1b.

Experiment 1b improved upon Experiment 1a by making the room only cue a less precise cue to navigation and by increasing the target sample size from 40 to a more conservative sample size of 60. Doubling the size of the room and removing the room ceiling resulted in single-cue variabilities that were no longer significantly different. This indicates participants were able to use optic flow with similar precision to the room-shape cue when navigating to a previously visited location. With more similar single-cue variabilities, evidence of cue integration was found in Experiment 1b. Further analyses indicated that actual cue weights (calculated using Equation 3) were not significantly different from the calculated optimal cue weights (calculated using Equations 1 and 2) and actual standard deviations in the dual-cue conditions were not significantly different from predicted optimal standard deviations using participant actual cue weights (calculated using Equation 4). However, the cue combined condition was found to show suboptimal standard deviation of responses when compared to the optimal standard deviation calculated using optimal cue weights rather than actual cue weights. This may be due to slight numerical differences in participant actual weights as compared to their predicted optimal weights. Given the substantial odds indicating that actual and optimal cue weights were not different, and the odds favoring the similarity of actual and optimal standard deviations in the dual-cue conditions, it appears participants optimally combined room shape and optic-flow cues when navigating in a desktop virtual environment in Experiment 1b.

Taken together, the results of Experiment 1 indicate that adult humans are able to optimally combine room shape and optic-flow cues when navigating in a desktop environment, at least when the variabilities associated with each cue in isolation are similar. It is possible that optimal integration also occurs when there is a large discrepancy in cue variabilities (as in Experiment 1a), however, cue combination becomes more difficult to detect as the single cues become more dissimilar, due to response capture from the more reliable cue (Ernst & Banks, 2002). Future experiments may be able to detect these differences by increasing sample size and, thus, increasing power.

Experiment 1 provides further support that adults can navigate through the use of optic flow alone in absence of body-based path integration cues (Kearns et al., 2002; Kirschen et al., 2000; Riecke et al., 2002) which is important for both a theoretical understanding of path integration cues and for the application of path integration research to navigation in desktop virtual environments. Additionally, although previous research has indicated a greater reliance on body-based path integration cues when combining body-based and optic-flow cues (Butler et al., 2010; Campos et al., 2010; Fetsch et al., 2009; Kearns et al., 2002), Experiment 1 has demonstrated that optic flow can nonetheless be weighted in an optimal fashion with an environmental cue in the absence of body-based path integration cues. The lack of clear cue combination in Experiment 1a along with the optimal cue combination found in Experiment 1b indicate that the relative variability of two single-cue conditions may be important for the optimal combination of cues.

While there are many further experiments that could be conducted examining the combination of path integration cues to navigation with each other and with environmental cues, there are often multiple environmental cues available for use when navigating to goal locations. To our knowledge, multiple environmental cues have not been examined in terms of their optimal integration. Experiment 2 examines the use of a geometric (room shape) cue and a landmark (cabinet) cue in the absence of useful path integration cues. Experiment 2 will determine whether two environmental cues to navigation are optimally combined similarly to an environmental cue and path integration.

CHAPTER 3. EXPERIMENT 2

Previous experiments examining the combination of multiple cues to navigation have focused on the combination of a piloting cue (landmarks or geometric cue) and path integration (Nardini et al., 2008; Sjolund, 2014; Zhao & Warren, 2015b) or on the combination of idiothetic and allothetic path integration cues to navigation (Butler et al., 2010; Campos et al., 2010; Fetsch et al., 2009; Kearns et al., 2002). However, in naturalistic navigation, there are often multiple piloting cues available that could be used to remember a learned goal location. For example, a typical classroom would have the shape of the room (a geometric cue) as well as a variety of possible landmark cues (e.g., chairs, desks, projector screen). Any or all of these cues may be used in combination to determine current position and goal locations. The second experiment will determine whether two piloting cues to navigation are combined in a Bayesian optimal manner to improve precision when returning to a previously visited location. In experiments testing the adaptive combination model, Ratliff and Newcombe (2008) found that weights of two piloting cues were adjusted based on relative cue reliability and salience, but their paradigm was unable to test whether cues were optimally combined because they did not include all four of the required conditions for determining optimality: two single-cue conditions, a combined condition, and a conflict condition. In Experiment 2, it was predicted that two piloting cues would be combined in a Bayesian optimal manner; however, it is possible that path integration, which may function as a back-up system for navigation (see Cheng et al., 2007, for review), uniquely contributes to the ability to optimally combine cues when navigating. Geometric and landmark cues, in contrast to path integration, may experience blocking and overshadowing, which could interfere with their combination.

Geometric cues are often preferred over landmark cues when cues are placed in a conflict (Cheng, 1986), but landmarks may be preferred over geometric cues when the landmark cue is especially salient (Ratliff & Newcombe, 2008). A related area of research examining the use of geometric and landmark cues involves classic associative learning effects, such as blocking and overshadowing. Blocking occurs when the relationship between one cue and an outcome is learned before the introduction of a second cue. In other words, after learning has occurred with the first cue, a second cue is added and associated with the same outcome. Learning the relationship between the first cue and a goal/outcome often prevents learning of the association with the second cue (Kamin, 1969). Overshadowing is a similar phenomenon in which two cues and their association to an outcome are learned concurrently. In contrast to blocking, in which a second cue is added after learning with the first cue, overshadowing occurs when two cues to a goal or outcome are available at the same time during learning. Testing occurs with each of the two cues in isolation to determine the level of learning associated with each cue. The typical overshadowing effect shows reduced learning to one or both cues when learned concurrently compared to when the cues are learned independently (see Kamin, 1969; Pavlov, 1927).

Some authors have failed to find evidence of blocking or overshadowing of geometric cues (primarily boundaries) with landmark cues (McGregor, Horne, Esber, & Pearce, 2009; Redhead & Hamilton, 2007; 2009). There are a variety of possible reasons for the lack of blocking and overshadowing of geometric cues (see Cheng et al., 2013, for review), one of which is that geometric and landmark cues may be processed in separate modules (McGregor et al., 2009). Due to the difficulty of interfering with the learning of geometric cues, it has been argued that geometric cues may be learned incidentally, and are therefore immune to blocking and overshadowing from non-geometric cues (Cheng, 1986; Gallistel, 1990; Redhead & Hamilton, 2007; 2009).

Doeller and Burgess (2008) examined blocking and overshadowing of circular boundary (geometric) and landmark cues when participants attempted to return to a previously visited target location in a desktop virtual environment. They found that blocking occurred for a landmark cue when the relationship between a target and a circular boundary cue was established prior to the introduction of the landmark cue. However, when this was reversed such that the association between a landmark and a target location was learned first, the later introduction of a boundary cue did not indicate blocking. Similarly, when both a boundary and a landmark were learned concurrently, the landmark did not overshadow the boundary while the boundary overshadowed learning of the landmark. The authors additionally manipulated the size of the landmark in an attempt to influence its salience but this resulted in no effect on overshadowing. Thus, they concluded that landmarks can be blocked and overshadowed, but boundaries (a geometric cue) are immune to these effects. It is important to note that, while some overshadowing of the landmark learning occurred in Doeller and Burgess (2008), learning still occurred for both cues. The results of Doeller and Burgess (2008) support the hypothesis that participants in Experiment 2 would be capable of learning the relationship between each cue and a target location, but that the geometric cue will likely receive a greater relative weight during cue combination than the landmark cue.

While authors have argued that there may be preferential encoding of geometric information (Cheng, 1986; Gallistel, 1990), other authors have argued that geometric cues are not preferentially encoded and are therefore not immune to the effects of blocking and overshadowing (Austen, Kosaki, & McGregor, 2013; Austen & McGregor, 2014; Buckley, Smith, & Haselgrove, 2014; Kosaki, Austen, & McGregor, 2013; Wilson & Alexander, 2008; 2010). Contrary to the findings of Doeller and Burgess (2008), there is evidence that salience does influence blocking and overshadowing of geometric cues when landmark cues are sufficiently salient (Buckley et al., 2014; Kosaki et al., 2013; Redhead, Hamilton, Parker, Chan, & Allison, 2013). Wilson and Alexander (2010) suggested that the reason Doeller and Burgess (2008) found no evidence of blocking and overshadowing of geometric cues by landmark cues may be due to the uniform circular enclosure used in their experiments. Geometric boundaries that contain corners and other disambiguating features may not be immune to blocking and overshadowing because of reliance on individual corners or features rather than the shape as a whole when travelling to a remembered goal location (Wilson & Alexander, 2010). Therefore, rectangular enclosures used in the proposed experiments should not overshadow learning based on landmarks.

Buckley et al. (2014) trained participants to navigate to a target location over a series of trials. For the first phase of the experiment, the target location could be found by learning its association with either the shape of the enclosure or with landmarks within the enclosure that moved from trial to trial. In the second phase of the experiment, participants again learned to locate a target location using either the shape of a novel enclosure or novel landmarks. Buckley et al. (2014) found that when the relevant cue (enclosure shape or landmarks) was consistent from the first to second stage (intradimensional shift) learning occurred faster than if the cue was inconsistent across stages (extradimensional shift). This suggests that geometric cues may not have a preferred status in location learning, and that prior experience influences the salience of cues. Findings regarding cue salience are generally consistent with the previously mentioned adaptive-combination model, although creating a model to explain the complex relationship between geometric and landmark cues would benefit from further research (Cheng et al., 2013). The adaptive-combination model (Newcombe & Huttenlocher, 2006) states that preference for a landmark or a geometric cue will be determined by the relative weight associated with each cue.

The results of previous research indicate that landmarks and geometric cues may be differentially preferred based on their relative reliability and salience, thus it was hypothesized that these variables would also be related to their relative weights when used in combination. Because Experiment 2 incorporated a rectangular geometric cue (Wilson & Alexander, 2010), salience is determined in part by experience with cues (Buckley et al., 2014; Ratliff & Newcombe, 2008), and participants learned during practice trials that both cues were relevant, it was not expected that results would be influenced by overshadowing of cues. Therefore, Experiment 2 examined the use of geometric and landmark cues to navigation to determine if their combination is optimal from a Bayesian perspective. It was hypothesized that the combination of a geometric and a landmark cue would be similar to the predicted optimal performance based on Equations 1, 2, and 3. Additionally, it was hypothesized that the geometric cue would be a relatively more salient cue to navigation than the landmark cue and this differential salience would be reflected in a higher weight being assigned to the geometric cue, as determined in a cue conflict condition.

Method

Participants

Sixty-five undergraduate students (38 female, 27 male) from Iowa State University participated for course credit. One additional participant failed to complete the study due to simulator sickness. One additional participant was removed from analyses because he reported noticing the conflict condition. Trial responses were removed if participants responded in the direction opposite of the target direction, likely indicating they had a lapse in attention and did not turn around prior to response. Ten individual trials (<1% of total trials) were removed for response in the opposite direction (five from the combined condition, two from the room only condition, and four from the landmark only condition). A trial response was considered outlying if it fell three times the interquartile range above the third quartile of response distance from mean response location, and this was calculated separately for each of the four conditions. Seven trials were removed as outliers (<1%; three from the combined condition, two from the room only condition, and two from the conflict condition). Two participants were removed from analyses due to multiple outlying responses that prevented calculation of standard deviation in at least one of the four conditions.

Procedure

The procedure for Experiment 2 was identical to the procedure of Sjolund (2014) with three changes. First, instead of examining the combination of geometric and path integration cues to navigation in an immersive virtual environment, Experiment 2 examined the combination of geometric and landmark cues to navigation in a desktop environment (example view in Figure 10). The landmark was counterbalanced such that half of the participants experienced a landmark on the right side of the room while the other half experienced the landmark on the left side of the room. Landmark location did not change the overall pattern of responses. Thus, the four conditions of interest included room shape only (the landmark was removed before responding), landmark only (the room was removed before responding), both cues combined, and both cues in conflict (10° conflict between cue-indicated correct target locations[4]).

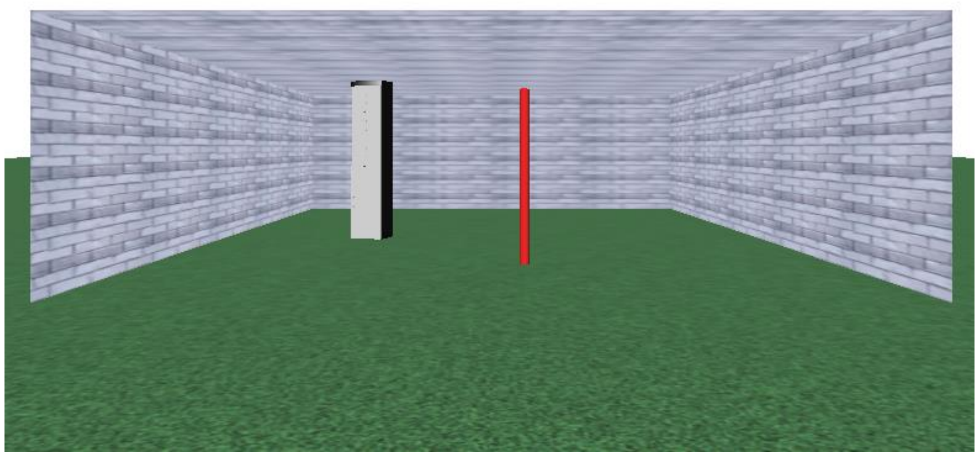


Figure 10. Example view from the start of a trial in Experiment 2.

Related to the first change, the second change was the addition of disorientation after every trial to render optic flow information useless for navigation to the target location. After every encoding of a new target location, participants appeared at a random location and orientation in front of the room/landmark prior to their response. By disorienting participant starting response location on every trial, the use of the landmark and/or room shape was necessary to reorient and travel to the correct target location.

[4] Pilot testing indicated that the majority of participants noticed the conflict at 15° but did not notice the conflict at 10°.

This allowed for the determination of the optimal integration of a geometric cue (room shape) and a landmark cue without optic flow being used as a cue for navigation. Therefore, Experiment 2 no longer examined the combination of a piloting cue to navigation (landmark or geometric cue) with path integration. Instead, Experiment 2 examined the combination of two piloting cues to navigation (geometric and landmark cue) without the influence of path integration.

Finally, as in Experiment 1, during the 15 second pause between encoding and response, participants performed a backward-counting task requiring numerical input using the computer keyboard. This backward counting task disrupted verbal and visual rehearsal strategies between encoding and response.

Aside from the aforementioned changes, the procedure for Experiment 2 was identical to that of Sjolund (2014). Experiment 2 included the four experimental conditions needed to determine whether two cues are combined in a Bayesian optimal manner. Two single-cue conditions (room only and landmark only) were included to allow for the calculation of Bayesian optimal cue weights using Equations 1 and 2 and predicted optimal standard deviation using Equation 4. A combined condition (room and landmark together) provided a measure of actual standard deviation to be compared with the predicted optimal standard deviation that was calculated using Equation 4. Finally, a conflict condition placed the correct target location indicated by the room in conflict with the correct target location indicated by the landmark. The relative proximity of participant responses to each of the two cue-indicated correct locations was used with Equation 3 to determine actual cue weightings. Actual cue weightings were compared with the optimal cue weightings predicted using the single-cue condition variabilities and Equations 1 and 2.

Results

Analyses followed those of Nardini et al. (2008), Sjolund (2014), and Experiment 1. Standard deviations based on absolute response distance (see Figure 11) were analyzed in a one-way ANOVA for response condition (combined, room only, landmark only, and conflict). The main effect of condition, with Greenhouse-Geisser correction, was significant, $F(3, 186) = 8.77$, $p < .001$, $\eta^2_G = 0.08$. To determine which of the two single-cue conditions had the lower response variability, a paired-samples *t*-test compared response standard deviation in the room only condition ($M = 0.44$, $SD = 0.24$) to the response standard deviation in the landmark only condition ($M = 0.55$, $SD = 0.38$). Response standard deviation in the room only condition was not significantly lower than response standard deviation in the landmark only condition $t(62) = 2.00$, $p = .05$, but was marginally significant. It was predicted that the response standard deviation in the cue combined condition would be lower than those in either of the single-cue conditions. Planned contrasts revealed that response standard deviation in the cue combined condition ($M = 0.35$, $SD = 0.22$) was significantly lower than standard deviation in the room only condition, which was the single-cue condition with numerically less variability $F(1, 62) = 6.20$, $p < .05$, $\eta^2_G = 0.04$. The cue conflict condition ($M = 0.37$, $SD = 0.21$) was also significantly less variable than the room only condition $F(1, 62) = 4.42$, $p = .04$, $\eta^2_G = 0.02$. Response standard deviation was significantly lower in both dual-cue conditions compared to the room only condition, which was the less variable of the two single-cue conditions. This suggests that participants were combining cues to improve navigation precision.

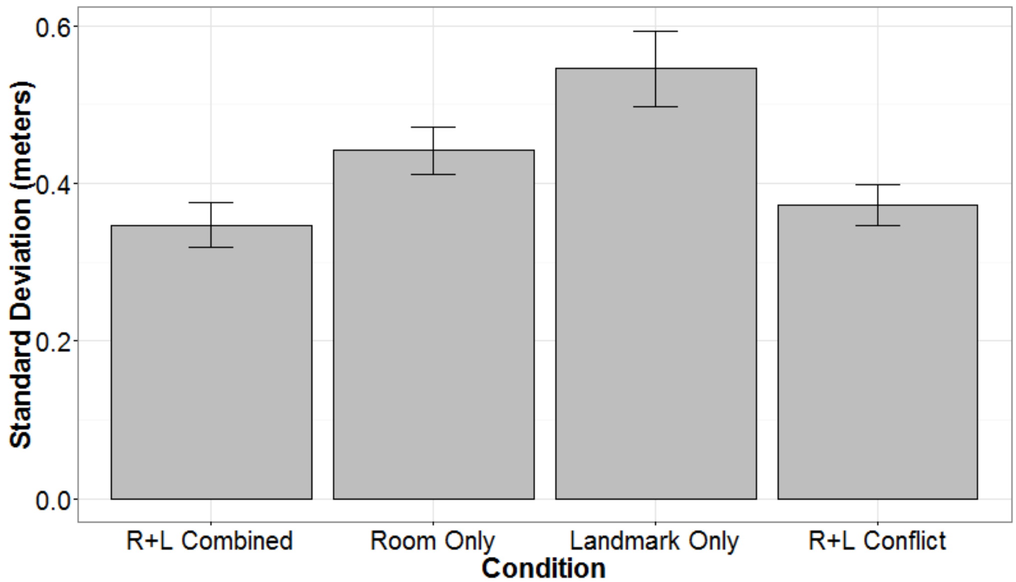


Figure11 . Average response distance standard deviations as a function of condition in Experiment 2. Error bars represent +/- 1 standard error.

Optimal weights for the room shape and landmark only conditions were calculated for each participant using the variances from each of the single-cue conditions following Equations 1 and 2. Actual weights for room shape and landmark were calculated as the relative proximity of responses to the room-defined and landmark-defined target 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 weight (M = 0.56, SD = 0.28) and the actual weight (M = 0.48, SD = 0.07) were significantly different $t(62)$ = 2.18, p = .03, suggesting that participants did not assign optimal weights to the landmark and room when combining cues.

To determine whether there was a significant preference for the room-shape cue or the landmark cue in the conflict condition, the relative proximities of responses to the room shape-indicated correct location were 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 lower weight than 0.5, $t(62) = 2.72$, $p < .01$, indicating a significant preference for the landmark cue over the room-shape cue in the conflict condition. In contrast, a one-sample *t*-test comparing calculated optimal weights to 0.5 indicated that neither cue should receive significantly more weight if optimal integration were occurring $t(62) = 1.64$, $p = .11$. Bayesian analyses (JZS prior, scale *r* of 0.5 indicating a small expected effect) indicated strong odds in favor of the null at 5.23:1 (Gallistel, 2009; Rouder et al., 2009). Together, these results indicate that participants assigned more weight to the landmark cue than what optimal integration of cues would predict.

Figure 12 illustrates the comparison of 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. Importantly, each individual had his/her own model prediction curve, actual room weight, and standard deviation of responses in the conflict condition. Figure 12 uses the average room weights and standard deviations to display an average of the individual curves. Given the relatively large variability in predicted optimal room weight across participants, the predicted optimal standard deviation illustrated in the figure ($M = 0.35$) is higher than the mean calculated optimal standard deviation ($M = 0.29$).

Paired-samples *t*-tests compared each individual's actual standard deviation of

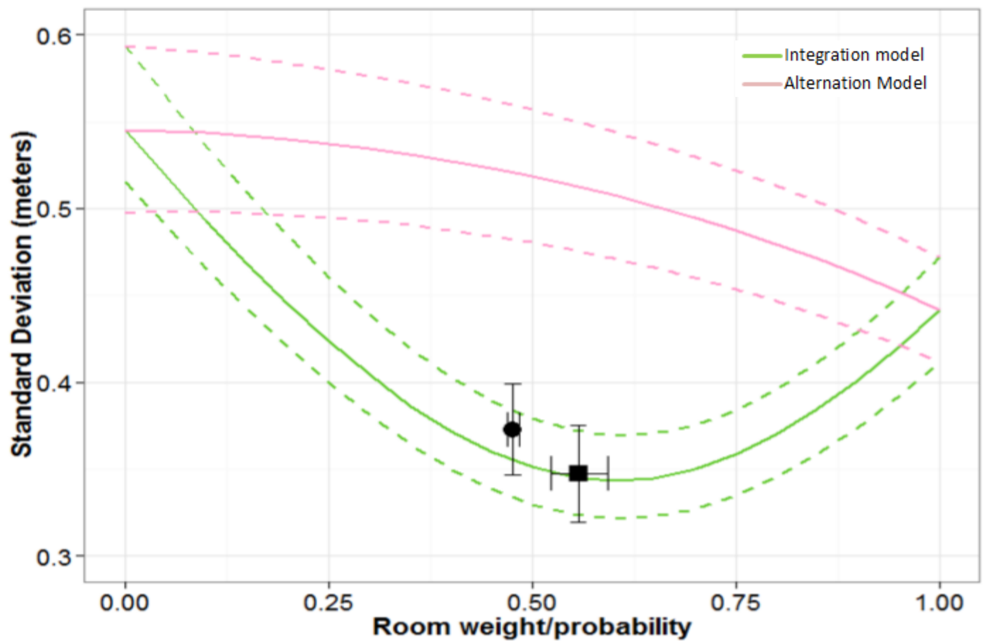


Figure 12 . Integration model predicted optimal standard deviation of responses across possible actual room weights and alternation model predicted standard deviation of responses across possible cue use probabilities from Experiment 2. The point indicating average actual weight and standard deviation of conflict condition responses is plotted (circle). The point indicating average optimal weight and standard deviation of the combined condition is also plotted (square). Error bars represent +/- 1 standard error.

responses in the dual-cue conditions to the standard deviation predicted using their calculated optimal cue weights and Equation 4. Participant actual standard deviation of responses in the conflict condition (M = 0.37, SD = 0.21) were significantly higher than their calculated optimal standard deviation of responses (M = 0.29, SD = 0.14), $t(62)$ = 3.16, p < .01. Participant actual standard deviation of responses in the combined condition (M = 0.37, SD = 0.21) were not significantly higher than their calculated optimal standard deviation of responses (M = 0.35, SD = 0.22), $t(62)$ = 1.85, p = .07, 95% CI [-0.12, 0.004]. However, Bayesian analyses (JZS prior, scale r of 0.5 indicating a small expected effect) indicate weak odds in favor of the null at 1.13:1 (Gallistel, 2009; Rouder et al., 2009). This indicates that response variability in the conflict condition is higher than the predicted variability if participants had been optimally combining cues, and response variability in the combined condition is not conclusively similar to predicted variability if participants had been optimally combining cues. Therefore, we do not have evidence that participant standard deviation of responses were consistent with optimal combination of cues.

A second set of paired-samples *t*-tests compared each individual's actual standard deviation of responses in the dual-cue conditions to the standard deviations predicted using their actual cue weights and Equation 4. Participant actual standard deviations of responses in the conflict condition were not significantly different from their predicted standard deviations given their actual cue weights (M = 0.38, SD = 0.19), $t(62) = 0.09$, $p = 0.92$, 95% CI [-0.05, 0.06]. Bayesian analyses (JZS prior, scale r of 0.5 indicating a small expected effect) indicated strong odds in favor of the null at 5.24:1 (Gallistel, 2009; Rouder et al., 2009). Participant actual standard deviation of responses in the combined condition also were not significantly different from their predicted standard deviation given their actual cue weights, $t(62) = 0.91$, $p = 0.37$, 95% CI [-0.03, 0.09]. Bayesian analyses (JZS prior, scale r of 0.5 indicating a small expected effect) indicate strong odds in favor of the null at 3.61:1 (Gallistel, 2009; Rouder et al., 2009). This suggests that participant response standard deviations are consistent with their predicted standard deviations, given that they did not assign optimal weights to the two cues.

Discussion

The second experiment examined the combination of room shape (a geometric cue) and a landmark cue in navigation. Previous research examining the combination of spatial cues to navigation has focused on the combination of a piloting cue and path integration cues (Nardini et al., 2008; Sjolund, 2014; Zhao & Warren, 2015b) or between multiple types of path integration cues (Butler et al., 2010; Fetsch et al., 2009). Experiment 2 adds to the current knowledge of cue combination by examining whether two piloting cues to navigation are also combined in a Bayesian optimal manner. It was hypothesized that geometric and landmark cues would be combined to reduce the variability in navigation responses when both cues were available. If optimal integration occurred, it was predicted that the room shape would be a more salient cue and would therefore receive a relatively higher weighting than the landmark.

The current results indicate that a geometric and landmark cue can be combined to reduce response variability when two cues are available, relative to single-cue conditions. Therefore, learning of the two cues together did not result in the complete overshadowing of one cue by the other. In fact, the response standard deviation in the room only condition was not significantly lower than the response standard deviation in the landmark only condition, indicating that the two cues were well balanced in terms of precision.

While response standard deviations were reduced when both cues were available, indicating that both cues were used to improve navigation precision, this combination was not consistent with Bayesian optimal predictions. The actual weight participants assigned to the room-shape cue was significantly lower than the predicted optimal weight calculated from the single-cue conditions using equations 1 and 2. The actual standard deviations of responses in the conflict condition were significantly higher than the predicted optimal standard deviations of responses using Equation 4. Additionally, while the actual standard deviations of responses in the combined condition were not significantly higher than the predicted optimal standard deviations, Bayesian analyses indicated weak odds in favor of the null. Taking these results in combination, there was little evidence that participants were optimally combining cues to reduce variability in the dual-cue conditions.

Contrary to prediction, the room-shape cue received significantly lower weight than the landmark cue. The actual room shape weight was significantly lower than the predicted optimal weight for the room-shape cue. Based on previous research regarding blocking and overshadowing of landmark cues by geometric cues, it was predicted that a suboptimal cue weighting would occur if the room-shape cue received greater weight than predicted optimal, opposite to what the results indicated. Together, the results showed a greater-than-optimal reliance on the landmark cue as compared to the room-shape cue in the dual-cue conditions, contrary to what blocking and overshadowing literature may suggest.

While some have suggested that geometric cues are learned incidentally, and therefore receive a privileged role in spatial memory and navigation (Cheng, 1986; Gallistel, 1990), others have argued that especially salient or reliable landmark cues may overshadow or block the learning of a geometric cue (Buckley et al., 2014; Kosaki et al., 2013; Redhead, Hamilton, Parker, Chan, & Allison, 2013). Experiment 2 provided additional evidence that the learning of a geometric cue does not necessarily overshadow the learning of a landmark cue. However, participants knew from the practice trials that both cues must be learned to navigate in single-cue conditions. It is possible that participants naïve to the single-cue conditions may show evidence of overshadowing due to differences in strategy.

The reason for sub-optimal weighting due to over-reliance on the landmark cue was unanticipated and should be examined through future research. There are several possible explanations for landmark over-reliance. First, the landmark cue may be an especially salient cue to navigation in the current experimental design, capturing participant attention and navigational strategies. Second, participants may have learned from the practice trials that both cues were important to the task, and may have altered their normal cue-weighting in anticipation of the need to remember both cues in relation to the target location.

Future research may attempt to vary the salience of the landmark cue to determine whether this influences cue weightings. For instance, changing the size, position, color, or reliability of the landmark cue may alter its weight relative to the room-shape cue. Additionally, future experiments could examine whether experimental design influenced cue weightings. For example, instead of experiencing each condition multiple times, participants could experience a "catch" trial that removes one cue or the other without their prior awareness that this trial would occur. This would require a between-subjects design to compare conditions, since repeated trials would not be possible, and would preclude the ability to determine whether individual cue weightings are optimal, but may allow for a determination of whether prior knowledge of single-cue conditions influences response strategy.

Experiment 2 indicated that a landmark and a geometric cue were used together to improve precision in dual-cue conditions, as evidenced by significantly lower standard deviations of responses in the dual-cue as compared to the single-cue conditions. However, this cue combination was not consistent with Bayesian optimal predictions.

Instead, participant responses indicated an overreliance on the landmark cue as compared to the geometric cue, as evidenced by an geometric cue weighting that was significantly lower than 0.5 (the cue weight associated with no preference). Future experiments should determine whether this overreliance on the landmark cue may be due to the relative salience of the landmark cue or to the specific experimental design of the current study.

Experiments 1 and 2 examined the combination of cues to navigation in a three-dimensional virtual environment; however, many spatial memory tasks also occur in two-dimensional environments. For example, remembering locations on a computer desktop or webpage is also a spatial memory task. Experiment 3 expanded the use of the Bayesian combination methodology to examine the use of a button and a rectangle cue in a two-dimensional desktop environment.

CHAPTER 4. EXPERIMENT 3

Experiments 1 and 2 examined the combination of cues to navigation in a three-dimensional virtual desktop environment. From a three-dimensional viewpoint, individuals are only able to see small, first-person snapshots of the whole environment layout at one time, which they must integrate to form a cognitive map of the space. This occurs in our daily life as we learn the layout of a new environment from walking around it. However, much of the desktop navigation we experience occurs from two-dimensional views of the display rather than from three-dimensional perspectives. From a two-dimensional viewpoint, people can see the configuration of the space all at once. This occurs when studying a map to learn the layout of a new environment. These two-dimensional environmental perspectives also have multiple cues within them that could be used to remember target locations, similar to what may be used in three-dimensional environments. For instance, when navigating a series of webpages, the pages are often set up with boxes of text (similar to geometric cues) and buttons or links (similar to landmark cues). It is unclear how these cues may be used in combination to remember target locations. The third experiment examined memory for spatial locations in a two-dimensional environment to determine whether multiple cues are combined in a Bayesian optimal manner.

Sequential viewing of an environment from a series of three-dimensional perspectives internal to the environment is referred to as route learning (e.g., walking through a new environment). Survey or map learning, in contrast, typically entails simultaneous viewing of an entire environment from a two-dimensional perspective external to the environment (e.g., studying a map). Differences in spatial memory acquired from two-dimensional and three-dimensional perspectives have been examined (Fields & Shelton, 2006; Moeser, 1988; Thorndyke & Hayes-Roth, 1982; Zhang, Zherdeva, & Ekstrom, 2014). Thorndyke and Hayes-Roth (1982) examined the spatial memory of individuals who learned an environment through studying a map as compared to those who learned through direct experience within the environment (ranging from 6-24 months of experience). They found that map learning resulted in more accurate estimates of Euclidean distance than direct route experience, although Euclidean estimates improved with greater route learning experience, to eventually reach the same level of map learning. In a similar study, Moeser (1988) found that, when a to-be-learned environment is especially complex, learning from a map resulted in greater spatial memory performance in distance and direction estimation than three years of route-learning experience. Fields and Shelton (2006) also found a benefit for survey over route learning in later spatial memory performance in cases of limited learning trials. Additionally, there are differences in the pattern of brain activation recorded during the encoding of route and survey representations (Shelton & Gabrieli, 2002; Shelton & Pippitt, 2007), suggesting a possible neural basis for behavioral differences.

Zhang et al. (2014) examined how spatial memory differs after learning from navigating a route or studying a map. Participants learned the layout of a virtual town either by studying an aerial view of landmark locations (map condition) or by travelling through the environment from a first-person perspective (route-learning condition). Participants then recalled the locations of objects within the virtual town through the use of judgements of relative direction (JRDs) and through a scene- and orientation-dependent pointing task (SOPs). JRDs entail taking on a perspective that is dependent on the relationship between landmarks and not on a viewpoint the observer experienced, while SOPs depend on an individual's current position within the environment (Zhang et al., 2014). A JRD task requires a participant to imagine standing at the location of one landmark, facing a second landmark, and, from that imagined perspective, point to where a third landmark would be located (e.g., "Imagine you are standing at the Campanile, facing the Memorial Union, point to the Library"). An SOP task, in contrast, would require a participant to point to a landmark from their current perspective (e.g., "Point to the Memorial Union building"). Zhang et al. (2014) found that those who studied a map performed better on the JRD task than those who studied the route, while the opposite was true for the SOP task. These results provide evidence that studying a landmark layout from a two-dimensional (map) perspective will lead to faster learning of landmark relationships than learning from a three-dimensional (route-learning) perspective. This is consistent with similar research conducted by Thorndyke and Hayes-Roth (1982), Moeser (1988), and Fields and Shelton (2006).

Similar to three-dimensional environments (see Kelly et al., 2008; Nardini et al., 2008; Sjolund, 2014), multiple cues to navigation may be used together to improve navigation performance in a two-dimensional virtual display. Fitting, Wedell, and Allen (2009) simulated a Morris water maze task in a two-dimensional desktop display. Participants viewed a circular field on a computer screen from an aerial perspective with one, two, or three landmarks available as cues, manipulated between-subjects. Participants used the computer mouse to navigate the image of a rat around the circular arena in search of a target location. Over a series of four trials, participants learned to navigate the rat image to a target from various starting locations outside the circular field.

After four learning trials, 16 test trials measured navigation performance to the target location. Fitting et al. (2009) found that navigation performance improved as the number of landmark cues increased. This suggests that participants were able to use multiple landmark cues together to improve memory for the goal location. However, it is unclear whether the combination of cues in a two-dimensional environment conforms to predicted Bayesian optimal integration.

The research conducted by Fitting et al. (2009) follows the methods of category prototype research, which examine how individual objects are represented in memory. In these experiments, participants are asked to remember the location of an object in the environment (or in a drawing) and are later asked to replace that object in its original location. Huttenlocher, Hedges, and Duncan (1991) examined memory for dots in a circle by requiring participants to view the location of a dot and later replace the dot in the original location. Huttenlocher et al. found that participant response locations showed a bias toward the center of the circle quadrants (i.e., responses fell closer to the center of the quadrants than the true target locations). It is hypothesized that this represents a Bayesian process for remembering location in which fine grain memory for the object location is combined with categorical information regarding quadrant prototype locations.

Huttenlocher et al. (1991) examined responses to the dot location task using a model called the basic Category Adjustment Model (CAM). This approach assumes that the expected value of a response $E[R]$, can be represented as a weighted average of fine-grain and categorical information as described in the following equation:

$$E[R] = \lambda\mu + (1 - \lambda)p \tag{6}$$

where μ is the mean of the distribution of fine-grain memories for the object (the true location of the object because it is assumed to be unbiased), p is the mean of the distribution of prototype locations for a category (e.g., the upper-left quadrant), and λ is the relative weight of the fine-grain information (varies from 0 to 1). This model has also been modified to account for flexible category weightings (Fitting, Wedell, & Allen, 2007), such that different categorical information can receive different relative weight. Similar to the Bayesian integration examined in Experiments 1 and 2, it has been found that fine-grain and categorical information are combined in a weighted fashion when remembering the location of a dot on a two-dimensional circular field (Fitting et al., 2007; Huttenlocher et al., 1991). Therefore, it seems appropriate to use Bayesian methods to evaluate cue combination in two-dimensional environments.

Although there are some differences in the behavioral spatial memory performance after (Fields & Shelton, 2006; Moeser, 1988; Thorndyke & Hayes-Roth, 1982; Zhang et al., 2014) and neural activation during (Shelton & Gabrieli, 2002; Shelton & Pippitt, 2007) two-dimensional and three-dimensional encoding of an environment, both methods of encoding lead to learning of the relationships between cues and generally accurate performance on spatial memory tasks (Fields & Shelton, 2006; Moeser, 1988; Thorndyke & Hayes-Roth, 1982; Zhang et al., 2014). Fitting et al. (2009) found that providing multiple cues to navigation increased performance on a target location learning task as compared to one cue in a two-dimensional environment, suggesting the use of multiple cues together to improve spatial memory performance. However, Fitting et al. (2009) did not include the four conditions required to determine whether the combination of multiple cues was optimal from a Bayesian perspective (two single-cue conditions, a combined condition, and a conflict condition). Experiment 3 examined whether the combination of cues in a two-dimensional environment occurs in a Bayesian optimal manner, similar to the combination of cues to navigation in a three-dimensional environment.

Method

Participants

Fifty-four undergraduate students (27 female, 27 male) from Iowa State University participated for course credit. Two additional participants were removed from analyses because they reported noticing the conflict condition. A trial response was considered outlying if it fell three times the interquartile range above the third quartile of response distance from mean response location, and this was calculated separately for each of the four conditions. Seventy-nine trials were removed as outliers (3% of total trials; spread across all four conditions).

Procedure

The third experiment was a similar, but simplified, version of the task completed in Experiments 1 and 2. Experiment 3 blended the procedures used by Nardini et al. (2008), Sjolund (2014), and Experiments 1 and 2, with the dot-replacement procedures used in the category prototype literature (Fitting et al., 2007; Fitting et al., 2009; Huttenlocher et al., 1991). First, instead of navigating through a three-dimensional virtual environment, participants were asked to remember the location of a target in a two-dimensional environment with a three-sided rectangle and a blue triangle as cues to location (Figure 13). Participants were asked to remember the location of a single red target dot while both the rectangle and the triangle were in view, with the knowledge that they would be asked to recall the target dot location after a 15 second backward counting task.

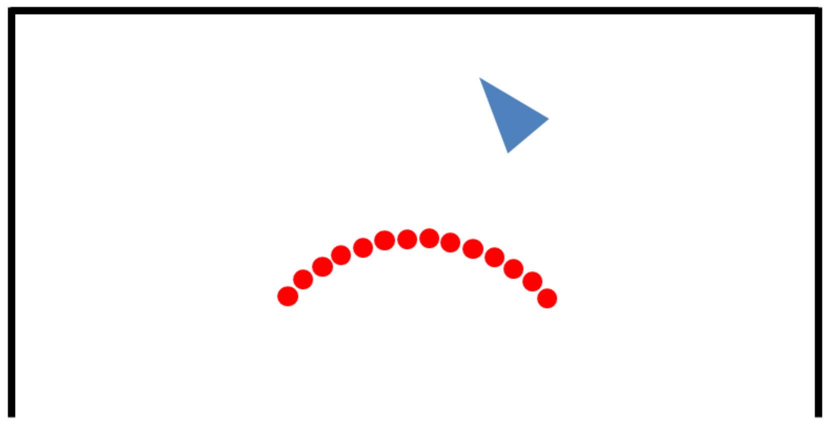


Figure 13. Stimuli used in Experiment three. Participants encoded the location of a target dot in relation to the three-sided rectangle and a blue triangle (in the current location or its mirror image across the vertical center). Red dots indicate target dot locations.

Target dots were chosen from one of 14 locations, equidistant from the starting cursor location on each trial. These 14 target dots and their relationship to the rectangle were similar to the targets used by Sjolund (2014) and Experiments 1 and 2 (Figure 1). The relationship between rectangle width and the possible target locations was analogous to the width of the large room condition from Sjolund (2014) and Experiments 1 and 2. The relationship between the height of the rectangle and the possible target locations was analogous to the depth of the small room condition from Sjolund (2014). The smaller relative height of the rectangle allowed for greater movement of the stimuli on the screen when participants were asked to recall the target dot location, preventing the use of the physical computer monitor as a cue to target location.

The red target dot was displayed for five seconds before the participant was allowed to move the cursor toward the target location. This five second delay encouraged accurate encoding of the target location in relation to the rectangle and the blue landmark triangle. After five seconds, participants were allowed to click on the target dot location, which was followed by a 15 second pause with both cues to the target dot location removed. During the 15 second break, participants completed a backward-counting task, requiring numerical input to the computer, to hinder verbal rehearsal strategies.

When the 15 second distractor task was finished, participants were asked to use the computer mouse to click in the location of the previously viewed target. Responses occurred in one of four conditions: rectangle only, triangle only, cues combined, or cues in a seven degree conflict[5]. To prevent reliance on the edges of the physical monitor display to determine target location, the location of the rectangle and triangle on the desktop screen changed between study and response on every trial, while maintaining the relationship between the rectangle and triangle. Participants were instructed to remember the target dot location in relation to the three-sided rectangle and the blue triangle, while ignoring the edges of the physical desktop monitor. After a practice trial of each trial type, participants completed 12 blocks of trials consisting of one of each trial type appearing in a random order. The increase from four blocks (used in Experiments 1 and 2) to 12 blocks in Experiment 3 approximately equated overall experiment time. Each block in Experiment 3 took less time to complete than blocks in Experiment 1 and 2 because participants were studying from an overhead, two-dimensional perspective,

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[5] While spatial memory performance is relatively similar after learning from two-dimensional and three-dimensional environments, the relationship between cues is learned more quickly in a two-dimensional environment as compared to a three-dimensional environment (Fields & Shelton, 2006; Moeser, 1988; Thorndyke & Hayes-Roth, 1982; Zhang et al., 2014). This rendered the 15 degree conflict too noticeable to remain a sub-threshold cue shift. Pilot testing indicated that a 15 degree conflict was noticed but a 7 degree conflict was not noticed by the majority of participants.

rather than navigating in a three-dimensional perspective. The standard deviations of responses in each condition over multiple trials were analyzed to determine whether there was evidence of combination of the rectangle and triangle cues for remembering the target location.

Although Experiment 3 required a slightly different procedure than Experiments 1 and 2, the basic experimental conditions were the same for determining the optimality of cue integration. Experiment 3 included the four experimental conditions needed to determine whether two cues are combined in a Bayesian optimal manner. Two single-cue conditions (rectangle only and triangle only) were included to allow for the calculation of Bayesian optimal cue weights using Equations 1 and 2 and predicted optimal standard deviations using Equation 4. A combined condition (rectangle and triangle together) provided a measure of actual standard deviations to be compared with the predicted optimal standard deviations that were calculated using Equation 4. Finally, a conflict condition placed the correct target location indicated by the rectangle in a seven degree conflict with the correct target location indicated by the triangle. The relative proximity of participant responses to each of the two cue-indicated correct locations could then be used with Equation 3 to determine actual cue weightings or with Equation 5 as an estimate of the probability of the use of each cue when alternating between cues.

Results

Initial analyses followed those of Nardini et al. (2008), Sjolund (2014), and Experiments 1 and 2. Response error patterns showed a linear bias such that responses tended to fall down and to the left or up and to the right when compared to the correct target location[6]. This relationship was characterized by calculating the Fisher's (1921) z-transformed correlation between errors in the X-dimension and errors in the Z-dimension for each subject in each condition.

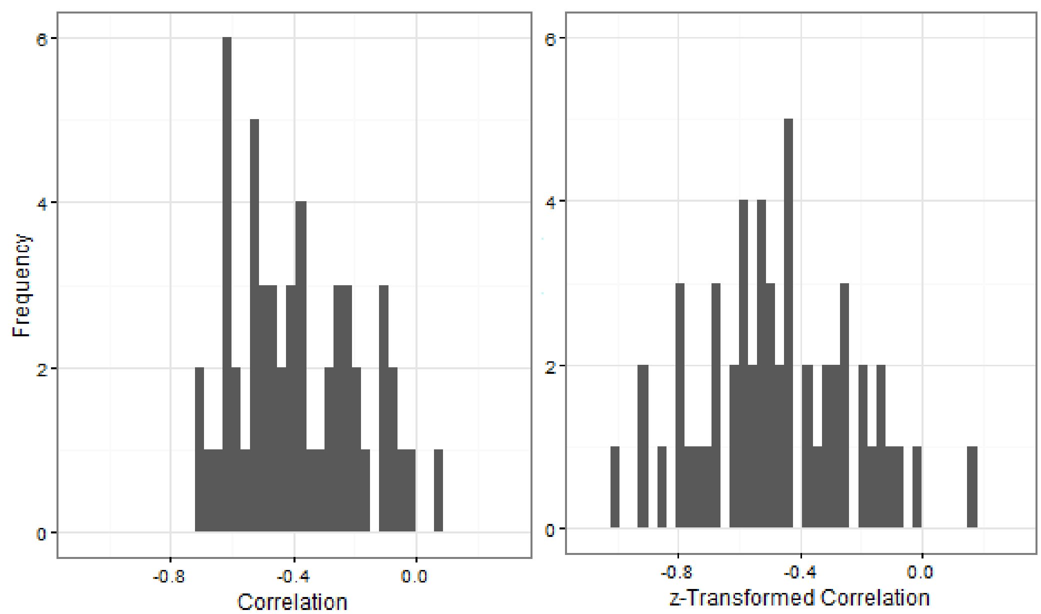

Figure 14. Non-transformed correlation (*r*) values for participant errors in the X- and Z-dimensions (left panel). Fisher *z*-transformed values for participant errors in the X- and Z-dimensions (right panel).

The Fisher's (1921) *z*-transformation was utilized due to the skewed distribution of *r* correlation coefficients as they approach ±1 (see Figure 14 for *r* and *z*-transformed correlation distributions in the current experiment). The skew in *r* correlation

[6] Because of the coordinate system used when displaying targets (such that (0, 0) is placed at the top-left of the computer screen), the relationship appears as a negative correlation in analyses.

distributions results in an underestimation of population correlations, even for large sample sizes (Fisher, 1921; Silver & Dunlap, 1987). Fisher's (1921) *z* transformation corrects the skewed distribution of *r* using the formula:

$$z = 0.5ln[(1 + r)/(1 - r)] \tag{7}$$

The mean Fisher's *z*-transformed values may also be backtransformed to *r* using the equation:

$$r = (e^{2z} - 1)/(e^{2z} + 1) \tag{8}$$

The backtransformed average *z*-transformed value is less biased than the average *r* value, especially for small sample sizes (Silver & Dunlap, 1987).

A one-sample t-test indicated that the mean z-transformed correlation for each subject (M = -.47, SD = 0.25; backtransformed r = -0.44) was significantly different from zero, indicating a significant relationship between X- and Z-dimension errors, $t(53) = 14.00$, $p < .001$. While there is no theoretical reason to believe the landmark (triangle) location or response condition would influence this linear trend, these variables were examined as possible influencing factors on the correlation between errors in the X-dimension and errors in the Z-dimension. A 2x4 mixed-design ANOVA with the between-subjects factor landmark location (left, right) and within-subjects factor response condition (Combined, rectangle only, triangle only, conflict) revealed no main effect of landmark location, $F(1, 156) = 0.10$, $p = .75$, $\eta^2_G < 0.001$, and no main effect of response condition, $F(3, 156) = 0.12$, $p = .95$, $\eta^2_G < 0.01$. The mixed-design ANOVA revealed a significant interaction between landmark location and response condition, $F(3, 156) = 3.05$, $p = .03$, $\eta^2_G = 0.04$. This interaction appears to be driven by differences in patterns between landmark locations in the combined and conflict conditions (Figure 15), however, no post-hoc comparisons remain significant after incorporating Bonferonni adjustments to correct for multiple comparisons in these exploratory analyses.

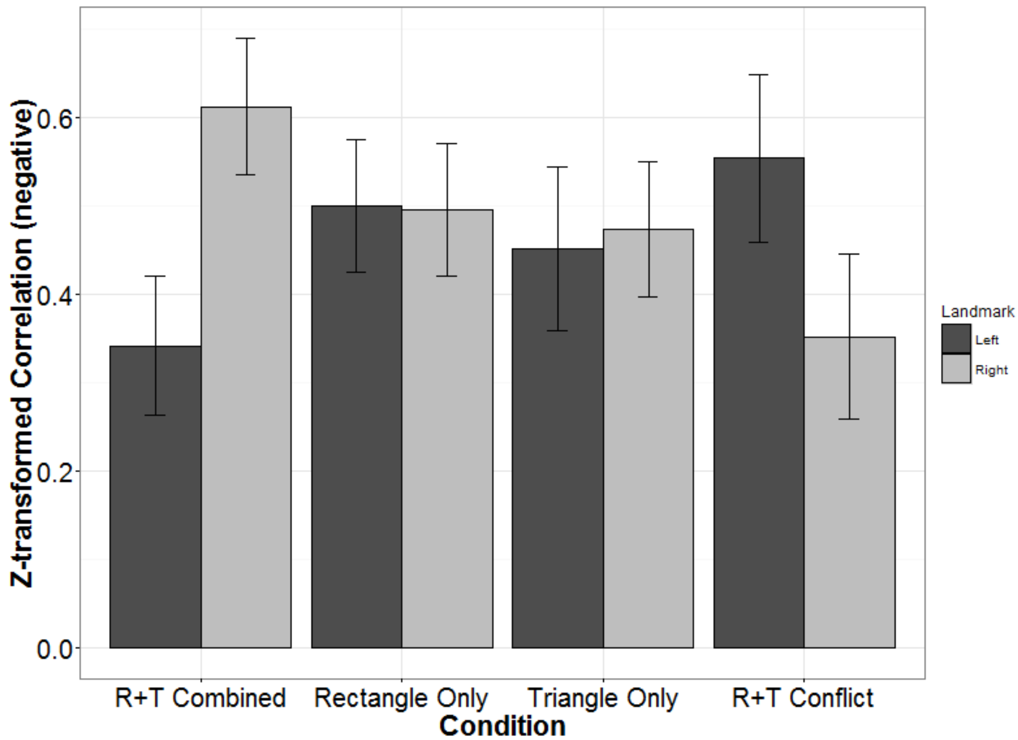

Figure 15. Average z-transformed correlations as a function of condition and triangle landmark location in Experiment 3. Error bars represent +/- 1 standard error.

Because the linear trend between errors in the X-dimension and errors in the Z-dimension was not explained by landmark location or by response condition, it is possible that the trend is related to hand movements when using a mouse with the right hand to record responses. To examine this possibility, pilot data collected using a circular landmark cue rather than a triangular landmark cue were examined. Aside from a different landmark cue (circle rather than triangle) and a different size rectangle cue (Figure 16), the stimuli and procedures were the same for the pilot experiment as they were for the current experiment. Nineteen participants completed the pilot study using the circular landmark cue. Similar to the trend found in the current experiment, a one-sample t-test indicated that the mean z-transformed correlation for each subject (M = -.14, *SD* = 0.23, backtransformed *r* = -0.13) was significantly different from zero, indicating a significant relationship, *t*(18) = 2.52, *p* = .02. The similar trend in the circular landmark data suggests that the relationship between errors in the X-dimension and errors in the Z-dimension may be related to the use of a two-dimensional desktop display or to the use of a computer mouse to record responses. Additionally, handedness of the participant or other participant biases may influence this trend. Further research is needed to determine the cause of this pattern.

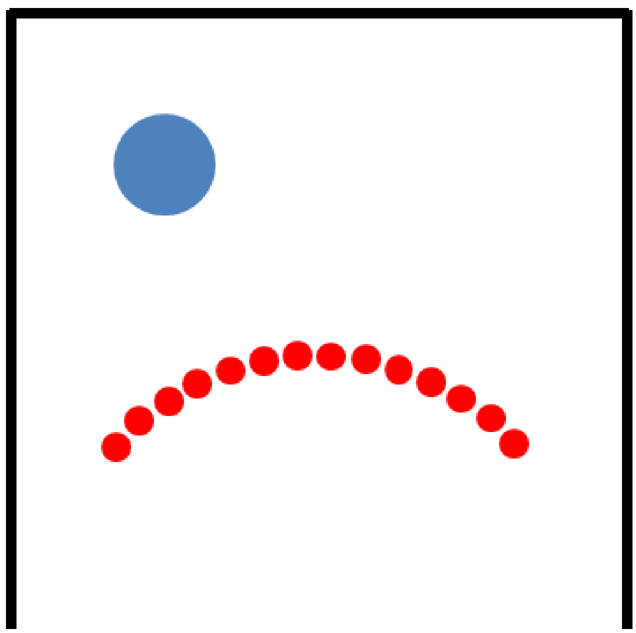

Figure 16. Stimuli used in a pilot study of Experiment 3. Participants encoded the location of a target dot in relation to the three-sided rectangle and a blue circle (in the current location or its mirror image across the vertical center). Red dots indicate target dot locations.

Because there were no clear explanations for the linear response error pattern, the results of Experiment 3 were analyzed as planned to determine whether participants combined cues to improve location memory precision. Standard deviations based on absolute response distance (see Figure 17) were analyzed in a one-way ANOVA for response condition (combined, rectangle only, triangle only, and conflict). The main effect of condition was significant, $F(3, 159) = 3.95$, $p < .01$, $\eta^2_G = 0.04$. It was predicted that the response standard deviations in the cue combined condition would be lower than those in either of the single-cue conditions. Planned contrasts revealed that the standard deviations in the cue combined condition ($M = 24.04$, $SD = 10.15$) were not significantly different from the standard deviations in the rectangle only condition ($M = 25.03$, $SD = 11.38$), which was the single-cue condition with less variability $F(1, 53) = 0.43$, $p = .51$, $\eta^2_G = 0.002$. The cue conflict condition ($M = 25.14$, $SD = 10.66$) was also not significantly less variable than the rectangle only condition $F(1, 53) = 0.005$, $p = .94$, $\eta^2_G < 0.001$. Thus, there was no evidence that participants were combining the rectangle and the triangle cues to improve precision when both cues were available. In other words, participants did not appear to be combining cues to improve spatial memory performance.

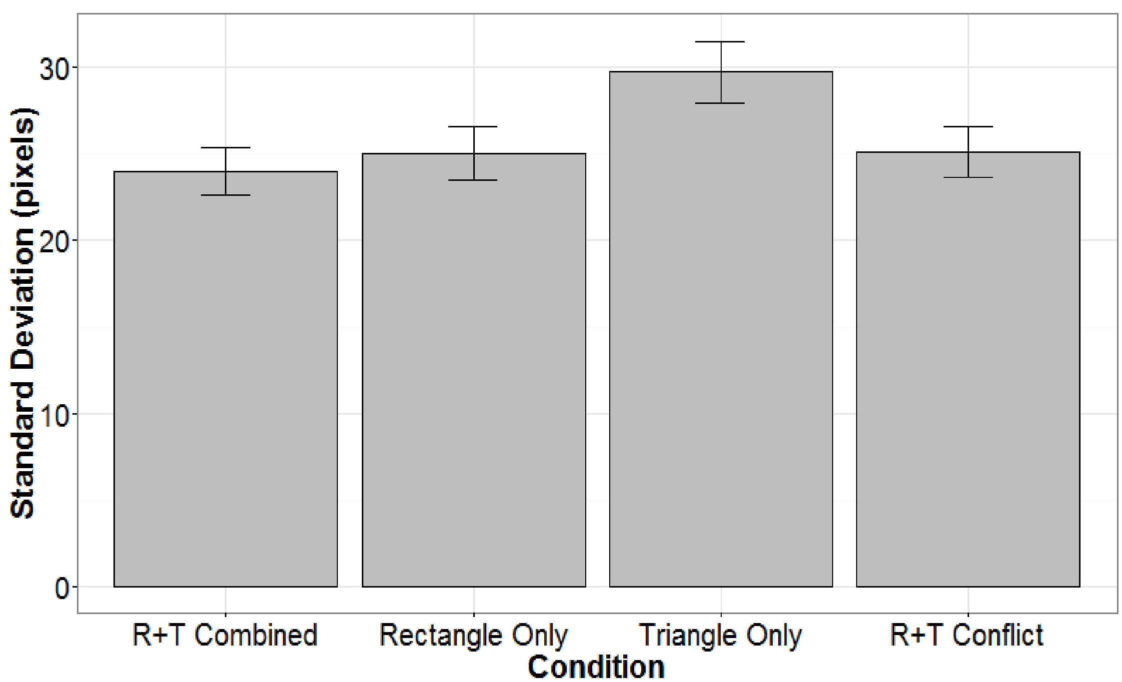

Figure17. Average response distance standard deviations as a function of condition in Experiment 3. Error bars represent +/- 1 standard error.

Participants did not appear to be combining cues to improve precision when both cues were available, therefore responses were compared to alternation model predictions to determine whether participants were alternating between rather than combining cues in Experiment 3 (see Nardini et al., 2008). Mean relative proximity to each of the cue-defined correct locations in the conflict condition (calculated using Equation 3) was used as an estimate of the probability of following each of the two cues when they indicate different correct target locations and their use is alternated. Using Equation 5, the predicted standard deviations in the combined cue conditions were calculated for each participant and compared to their actual standard deviations in each of the dual-cue conditions. The alternation standard deviations predicted by Equation 5 (M = 28.51, SD = 9.51) were significantly higher than the actual cue-combined standard deviations (M = 24.04, SD = 10.15), $t(53) = 3.08$, $p < .01$. The predicted alternation standard deviations were also significantly higher than the actual cue-conflict standard deviations (M = 25.14, SD = 10.66), $t(53) = 2.42$, $p = .02$. This suggests that participants did not respond in a manner consistent with the alternation model prediction for performance in the dual-cue conditions. In sum, performance in the dual-cue conditions was not consistent with cue combination (as evidenced by no improvement of precision in dual-cue compared to single-cue conditions) and was not consistent with cue alternation (as evidenced by the better precision in the dual-cue conditions than predicted alternation performance).

Because there was no significant difference between the rectangle only and the dual-cue conditions, there was no evidence that participants were combining cues to increase precision when both cues were available. In Experiment 1a, it was determined that participants with more similar precision in the two single-cue conditions also appeared to be combining cues to increase precision when both were available. This was tested in Experiment 3 by again performing a median split to separate the participants based on the absolute difference in standard deviation of distance responses between single-cue conditions (mdn = 4.05). Standard deviations based on absolute response distance for all subjects (see Figure 18) were analyzed using a 2x4 mixed-design ANOVA and there was no significant interaction between single-cue-condition similarity (similar, dissimilar) and response condition (combined, rectangle only, triangle only, conflict), $F(3,156) = 2.26$, $p = .08$, $\eta^2_G = 0.02$. There was a significant main effect of condition, $F(3,156) = 4.05$, $p < .01$, $\eta^2_G = 0.04$, and a significant main effect of similarity, $F(1, 52) = 4.89$, $p = .03$, $\eta^2_G = 0.04$, with the dissimilar group ($M = 28.29$, $SD = 8.59$) having a higher mean standard deviation than the similar group ($M = 23.69$, $SD = 6.57$).

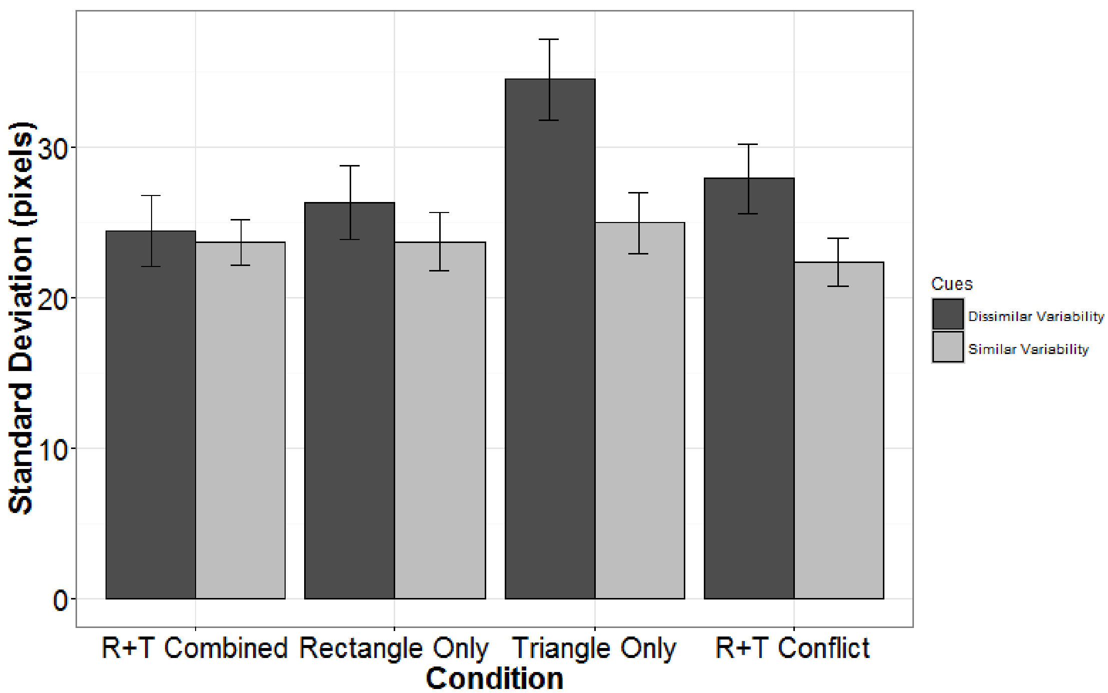

Figure 18. Average response distance standard deviations as a function of condition and single-cue relative variability in Experiment 3. Error bars represent +/- 1 standard error.

The lack of interaction between single-cue standard deviation similarity and response condition does not suggest that the lack of cue integration is due to a large discrepancy between the precision of the single-cue conditions. If the discrepancy between the single-cue conditions influenced cue combination, we would expect an interaction between similarity and condition, as was found in Experiment 1a. Further exploratory analyses examined whether the lack of cue integration may have been related to a floor effect, such that the precision of the better of the two single-cue conditions could not be improved upon in the dual-cue conditions.

To examine whether a floor effect may be preventing the integration of cues in Experiment 3, a median split (mdn = 26.11) separated the participants based on the average standard deviation of distance responses across all four conditions (combined, rectangle only, triangle only, conflict). Standard deviations based on absolute response

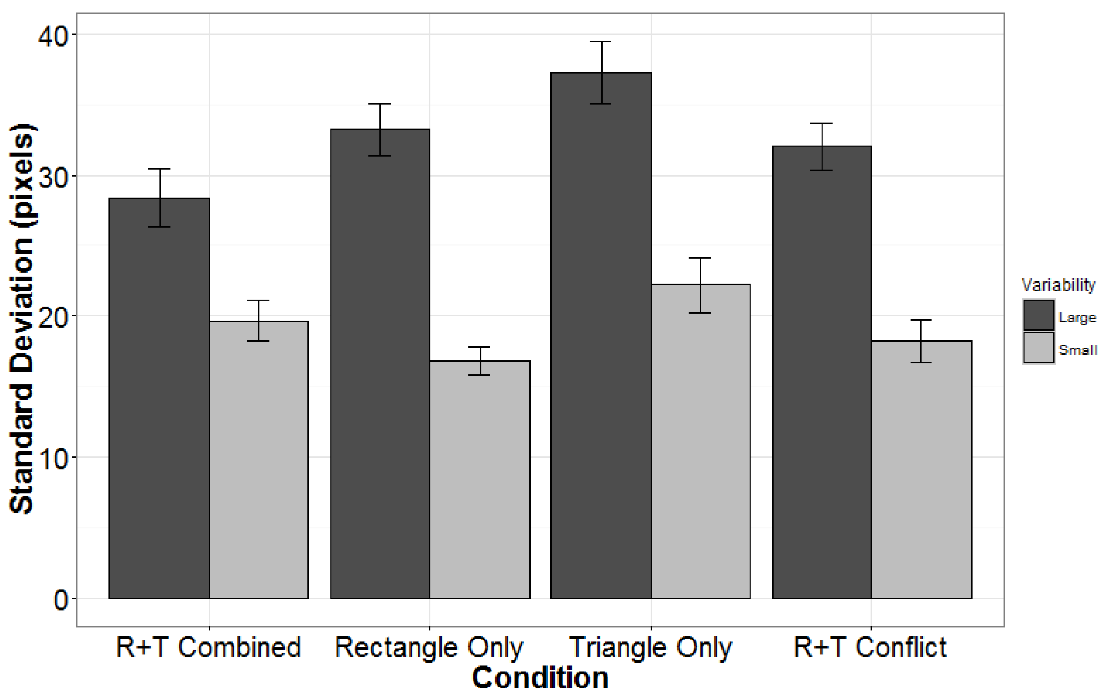

Figure 19. Average response distance standard deviations as a function of condition and overall mean variability in Experiment 1a. Error bars represent +/- 1 standard error.

distance for all subjects (see Figure 19) were analyzed using a 2x4 mixed-design ANOVA with Greenhouse-Geisser correction and found no significant interaction between overall variability (low, high) and response condition (combined, rectangle only, triangle only, conflict), $F(3, 156) = 1.72$, $p = .17$, $\eta^2_G = 0.03$. There was a significant main effect of condition, $F(3, 156) = 4.05$, $p < .01$, $\eta^2_G = 0.06$, and a significant main effect of variability, $F(1, 52) = 145.44$, $p < .001$, $\eta^2_G = 0.36$, with the more variable group ($M = 32.72$, $SD = 4.45$) having a higher mean standard deviation than the less variable group ($M = 19.25$, $SD = 3.72$).

Given the lack of significant interaction between mean variability (low versus high) and condition (combined, rectangle only, triangle only, conflict), it is unlikely that the lack of cue integration found in Experiment 3 is due to a floor effect. However, future research should examine whether increasing the difficulty of the task, thereby increasing overall response variability, encourages integration of cues.

Discussion

The results of Experiment 3 were inconclusive regarding the optimality of cue use in a two-dimensional desktop environment. There was no significant improvement in response precision when multiple cues were available compared to the more precise of the two single-cue conditions (rectangle-only condition), suggesting the two cues were not being combined to improve spatial memory precision. Additionally, results were not consistent with alternation between cues (using Equation 5). There are several possible explanations for the lack of clear cue integration or alternation, which should be examined in future studies.

In Experiment 1a, it appeared that the single-cue conditions were too discrepant to indicate integration of cues. Using a median split based on single-cue precision difference, Experiment 1a found that participants with more similar single-cue precision also appeared to be combining cues to navigation. A similar median split of the data from Experiment 3 did not indicate that relative precision in the single-cue conditions influenced cue combination. Further exploratory analyses examined whether the lack of integration may be due to a floor effect. Participant data were split based on the median overall average response variability and results again did not indicate that overall variability influenced the pattern of response distance standard deviation across conditions. In sum, the lack of cue integration found in Experiment 3 is unlikely to be due to a large discrepancy in the precision of the single-cue conditions or due to a floor effect.

In addition to the lack of cue integration found in Experiment 3, there was also an unexpected linear trend in response errors, such that responses tended to fall toward the bottom-left and top-right of the actual target location. This bias was not clearly related to the landmark triangle location (left or right) or response condition (combined, rectangle only, triangle only, conflict). Pilot data using a circular landmark target also suggested a significant correlation in errors in the X- and Z-dimensions, indicating this trend maybe caused by the use of a two-dimensional desktop display or a computer mouse. Future research should examine these variables as well as other variables, such as participant handedness, to determine their relationship to response bias in the current experiment.

In sum, the results of Experiment 3 were inconclusive in determining whether multiple two-dimensional cues can be combined in a Bayesian optimal manner to improve precision when remembering a previously learned target location. Results did not indicate a combination of cues, but also did not indicate alternation between cues. Experiment 3 illustrates the importance of testing multiple cue types and display modalities to determine their influence on cue combination. Future research should determine what factors may influence the combination of cues in a two-dimensional environment. This would elucidate whether cues are combined in a Bayesian optimal manner when navigating a desktop display or webpage.

CHAPTER 5. GENERAL DISCUSSION

Humans as well as non-human animals must navigate their environments to achieve their goals. Whether you are an adult human navigating from your apartment to your office, or if you are an ant navigating to find food, there are often multiple cues to navigation available for use. A question that has recently been posed is whether humans and non-human animals have the ability to use multiple cues to assist in reaching their navigation goals and whether this integration of cues occurs in a Bayesian optimal manner.

Sjolund (2014) extended the finding that landmarks could be optimally combined with path integration to improve navigation (Nardini et al., 2008) to find that optimal combination also occurs for a geometric cue (room shape) and path integration. However, there are many instances in which physical body movement is not possible when performing a navigation task. Experiment 1 built off previous research to determine whether idiothetic (body-based) path integration cues are required for optimal combination, or if allothetic optic-flow information provided by a desktop computer is sufficient for optimal combination.

Experiment 1a failed to find sufficient evidence that both optic-flow and room-shape cues were used to improve navigation precision in dual-cue conditions, which may have been due to a large discrepancy in precision in the single-cue conditions. The room-only condition had significantly lower standard deviations of responses than the optic-flow only condition. It is possible that this large discrepancy prevented optimal integration of cues. In contrast, optimal integration may have been occurring, but the weight given to the optic-flow cue may have been very small, making it difficult to detect the effect using the sample size of Experiment 1a (n = 41). Exploratory analyses indicated that participants who had more similar response standard deviations in the single-cue conditions also appeared to be using the cues to improve precision in dual-cue conditions. In contrast, the participants who had less similar response standard deviations in the single-cue conditions did not show evidence of using the two cues together to improve precision in the dual-cue conditions.

Experiment 1b improved upon Experiment 1a by making the room only cue a less precise cue to navigation. Doubling the size of the room and removing the room ceiling resulted in single-cue variabilities that were no longer significantly different. With more similar single-cue variabilities, evidence of cue integration was found in Experiment 1b. Further analyses indicated that actual cue weights (calculated using Equation 3) were not significantly different from the calculated optimal cue weights (calculated using Equations 1 and 2) and actual standard deviations in the dual-cue conditions were not significantly different from predicted optimal standard deviations using participant actual cue weights (calculated using Equation 4). However, the combined-cue condition indicated suboptimal standard deviation of responses when compared to the optimal standard deviation calculated using optimal cue weights rather than actual cue weights. This may be due to slight numerical differences in participant actual weights as compared to their calculated optimal weights. Given the substantial odds indicating that actual and optimal cue weights were not different, and the odds favoring the similarity of actual and optimal standard deviations in the dual-cue conditions, it was concluded that participants optimally combined room-shape and optic-flow cues when navigating in a desktop virtual environment in Experiment 1b.

Taken together, the results of Experiment 1 indicate that adult humans are able to optimally combine room-shape and optic-flow cues when navigating in a desktop environment, at least when the variabilities associated with each cue in isolation are similar. It is possible that optimal integration also occurs when there is a large discrepancy in cue variabilities (as in Experiment 1a), however, cue combination becomes more difficult to detect as the single cues become more dissimilar, due to response capture from the more reliable cue (Ernst & Banks, 2002). Experiment 1 provides further support, consistent with previous research (Kearns et al., 2002; Kirschen et al., 2000; Riecke et al., 2002), that adults can navigate through the use of optic flow alone in absence of body-based path integration cues. This is important for both a theoretical understanding of path integration cues and for the application of path integration research to navigation in desktop virtual environments. Additionally, although previous research has indicated a greater reliance on body-based path integration cues when combining body-based and optic-flow cues (Butler et al., 2010; Campos et al., 2010; Fetsch et al., 2009; Kearns et al., 2002), Experiment 1 has demonstrated that optic flow can nonetheless be weighted in an optimal fashion with an environmental cue in the absence of body-based path integration cues.

Previous research examining the combination of spatial cues to navigation has focused on the combination of a piloting cue and path integration cues (Nardini et al., 2008; Sjolund, 2014; Zhao & Warren, 2015b) or the combination of multiple path integration cues (Butler et al., 2010; Fetsch et al., 2009). The second experiment extended the findings of Bayesian optimal integration of a piloting cue with path integration cues (Nardini et al., 2008; Sjolund, 2014) to the combination of two piloting cues to navigation in the absence of path integration cues. Experiment 2 indicated that a geometric and landmark cue can be combined to reduce response variability when two cues are available, relative to single-cue conditions. However, contrary to prediction, this combination was not consistent with Bayesian optimal integration. The actual weight participants assigned to the room-shape cue was significantly lower than the predicted optimal weight calculated from the single-cue conditions using Equations 1 and 2, indicating a suboptimal overreliance on the landmark cue. The actual standard deviation of responses in the conflict condition was significantly higher than the calculated optimal standard deviation of responses using Equation 4. Additionally, while the actual standard deviations of responses in the combined condition were not significantly higher than the predicted optimal standard deviation, Bayesian analyses indicated weak odds in favor of the null. Taking these results in combination, there is little evidence that participants were optimally combining cues to reduce variability in the dual-cue conditions.

Experiment 2 illustrates that participants can use two piloting cues to navigation to improve response precision when both cues are available, although this combination is not necessarily consistent with the predicted optimal cue weighting. This experiment also provides evidence that the learning of a geometric cue does not always overshadow the learning of a landmark cue, providing insight into the debated relationship between the learning of geometric and landmark cues to navigation (Austen et al., 2013; Austen & McGregor, 2014; Buckley et al., 2014; Cheng, 1986; Cheng et al., 2013; Doeller & Burgess, 2008; Gallistel, 1990; Kosaki et al., 2013; Redhead & Hamilton, 2007; 2009; Redhead et al., 2013; Wilson & Alexander, 2008; 2010). Future experiments should determine whether this overreliance on the landmark cue may be due to the salience of the landmark cue or to the specific experimental design of the current study.

Finally, Experiment 3 examined the combination of cues in a two-dimensional desktop display, similar to what may occur when navigating a computer desktop or website. The results of Experiment 3 were inconclusive regarding the optimality of cue use in a two-dimensional desktop display. There was no significant improvement in response precision when multiple cues were available compared to better of the two single-cue conditions (rectangle-only condition). Future experiments should examine whether altering the task to increase overall response variability (e.g., reduce study time or alter stimuli) results in evidence of cue integration.

In addition to the lack of cue integration found in Experiment 3, there was also an unexpected linear trend in response errors, such that responses tended to fall toward the bottom-right and top-left of the actual target location. In other words, there was a significant correlation between X- and Z-dimension errors. This bias was not clearly related to landmark location (left or right) or response condition (combined, rectangle only, triangle only, conflict), however, a similar trend was found in a pilot study using slightly different stimuli. Future research should determine whether this relationship between X- and Z-dimension errors is related to the use of a desktop display, a computer mouse, or some other manipulation in the current experimental design.

Together, the current experiments expand the current knowledge regarding how multiple cues to navigation are used together to improve memory. Experiment 1a indicated the importance of the comparative precision of single cues to navigation, such that discrepant cues result in difficulty verifying cue combination. Experiment 1b balanced the single-cue-precision discrepancy found in Experiment 1a and illustrated that idiothetic (body-based) path integration cues are not necessary for optimal combination with a geometric environmental cue. Experiment 1b provided evidence that optic flow from a desktop was sufficient for optimal combination with a geometric cue.

Experiment 2 moved away from the study of path integration as a cue to navigation and instead examined the combination of a geometric and a landmark cue (two piloting cues) to navigation. While participants did improve their location memory precision when both cues were available compared to single-cue conditions, this reduction in variability was not consistent with the predicted optimal variability calculated from the single-cue conditions using Equation 4. Contrary to prediction, participants relied on the landmark cue significantly more than was calculated to be optimal. Thus, Experiment 2 illustrated that geometric and landmark cues can be used in combination, and that the geometric cue will not always overshadow the landmark cue. Additionally, the combination of geometric and landmark cues is not consistent with Bayesian optimal predictions, at least with the current set of stimuli. Future research should examine whether geometric and landmark cue combination can be optimal, and under what conditions this is likely to occur.

Finally, Experiment 3 examined the combination of cues in a two-dimensional desktop display rather than in a three-dimensional environment. It was found that participants did not improve their spatial memory precision when both a rectangle and a triangle cue were available, as compared to single-cue conditions, contrary to prediction. Additionally, performance in the dual-cue conditions was not consistent with the alternation model predictions calculated using response relative proximity to the two cue-indicated correct locations in the conflict condition (Equation 3) and Equation 5. Therefore, it is unclear whether participants were combining cues or alternating between cues in Experiment 3. The pattern of error responses also showed an unexplained linear trend that should be investigated in future experiments.

The current experiments indicate further study is needed, but illustrate the importance of testing a variety of stimuli when examining cue integration. Further research should examine the conditions under which two cues will be combined optimally and under which one cue may be assigned greater weight than calculated optimal. Additionally, future research should examine how cue combination is influenced by the type of cues available. For instance, it is possible that suboptimal cue weighting occurs more often for piloting cues to navigation, while a piloting and path integration cue may be more readily combined in a near-optimal fashion. Together, the current experiments expand the current knowledge regarding how multiple cues to navigation are used together to improve spatial memory and illustrate that small differences in stimuli may have a great impact on the ability to detect optimal cue integration.

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