

Cue combination in goal-oriented navigation

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Abstract

This study examined cue combination of self-motion and landmark cues in goal-localisation. In an immersive virtual environment, before walking a two-leg path, participants learned the locations of three goal objects (one at the path origin, that is, home) and landmarks. After walking the path without seeing landmarks or goals, participants indicated the locations of the home and non-home goals in four conditions: (1) path integration only, (2) landmarks only, (3) both path integration and the landmarks, and (4) path integration and rotated landmarks. The ratio of the length between the testing position (P) and the turning point (T) over the length between the T and the three goals (G) (i.e., PT/TG) was manipulated. The results showed the cue combination consistently for participants' heading estimates but not for goal-localisation. In Experiments 1 and 2 (using distal landmarks), the cue combination for goal estimates appeared in a small length ratio ($PT/TG=0.5$) but disappeared in a large length ratio ($PT/TG=2$). In Experiments 3 and 4 (using proximal landmarks), while the cue combination disappeared for the home with a medium length ratio ($PT/TG=1$), it appeared for the non-home goal with a large length ratio ($PT/TG=2$) and only disappeared with a very large length ratio ($PT/TG=3$). These findings are explained by a model stipulating that cue combination occurs in self-localisation (e.g., heading estimates), which leads to one estimate of the goal location; proximal landmarks produce another goal location estimate; these two goal estimates are then combined, which may only occur for non-home goals.

Keywords

Piloting; path integration; self-localisation; goal-oriented navigation; cue combination

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Significance statement

The current study demonstrated that participants combined self-motion cues and landmarks to estimate self-localisation prior to localising the home and non-home goals. However, proximal landmarks produce estimates for non-home goals rather than the home. These findings suggest that goal-oriented navigation and homing do not share the same mechanism.

Introduction

Navigation to a desired goal's location (goal-localisation) is a fundamental behaviour for all complex animals. The desired goal location can be a food source previously visited for animals (Morris et al., 1982) or a workplace for people living in modern society. Recent studies have discovered the neural bases of goal-oriented navigation (Brown et al., 2016; Chadwick et al., 2015; Howard et al., 2014; Sarel et al., 2017; Shine et al., 2019). The purpose of this article is to understand the cognitive mechanisms

regarding how people combine different cues available during navigation for goal-localisation.

Path integration refers to a method of using self-motion cues, including optic flow, to update representations of spatial relations between navigators and environments (Mittelstaedt & Mittelstaedt, 1982). People can use self-motion cues alone for goal-localisation. Without vision, people can keep track of previewed objects' locations during locomotion (Rieser, 1999). This process of updating self-to-object vectors using self-motion cues only is termed spatial updating (Klatzky et al., 1998; Rieser, 1989; Wang, 2017) or

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path integration (Collett et al., 1999; Etienne et al., 1998; Loomis et al., 1999; Philbeck et al., 2001). Thus, people can use path integration for goal-localisation.

Piloting refers to a method of using visual landmarks to determine locations of other objects (e.g., goals) and navigators (Etienne & Jeffery, 2004). People can also use only visual landmark cues for goal-localisation. Studies have shown that after disorientation, which disrupted path integration, participants could still use visual information to find goal locations (Doeller & Burgess, 2008; Hermer & Spelke, 1994; Zhou & Mou, 2016). Therefore, people can also use piloting for goal-localisation.

Despite decades of research on spatial navigation, we know little about how humans simultaneously utilise path integration (self-motion cues) and piloting (visual cues) in goal-oriented navigation beyond homing. Human spatial navigation studies have examined cue interaction in homing (e.g., Nardini et al., 2008). Participants walked a two-leg path and then walked back to the path origin with self-motion cues only, landmark cues only, and both these cues that could be consistent or conflicting in indicating the home location. Cue combination was supported if the variance of estimating error in a two-cue condition was reduced compared with that in single-cue conditions and was not different from the minimum variance of any linearly averaged estimates from single cues. Some studies examined the format of averaging the estimates from path integration and piloting: cue integration, cue alternation, or cue competition (e.g., Nardini et al., 2008; Zhao & Warren, 2015). Other studies examined the factors that could modulate the weights in averaging the estimates: cue reliability, cue stability, and navigators' spatial ability (e.g., Chen et al., 2017; Sjolund et al., 2018).

Instead of examining the format of cue interaction or factors modulating cue weights, Zhang et al. (2020) examined the stage of cue interaction: in determining navigators' heading and position (self-localisation) or homing. In their study, participants walked two-leg paths and then pointed to the origins of paths (i.e., home). The results showed that the cue combination in homing estimates only appeared when the length ratio of the second leg (L2) over the first leg (L1) of a path was small (L2/L1 length ratio=0.5) but disappeared when the length ratio was large (length ratio=2). In contrast, the cue combination in heading estimates appeared regardless of length ratios. Zhang et al. concluded that cue combination of path integration and piloting occurred in self-localisation but not in homing (self-localisation hypothesis). They also developed a mathematic model demonstrating that the cue combination in heading estimates could lead to the appearance of the cue combination in homing when the length ratio is small (e.g., length ratio=0.5) and the disappearance of the cue combination in homing when the length ratio is large (e.g., length ratio=2).

However, it is not clear whether the findings of cue interaction in homing can be extended to goal-oriented

navigation (home might be just one instance of goal). To tackle this issue, the current study investigated whether the stage of cue interaction in goal-oriented navigation is the same as in homing. We proposed and tested three hypotheses, respectively, stipulating cue interaction for goal-localisation only (late-combination), for self-localisation only (early-combination), and for both self-localisation and goal-localisation (dual-combination) (Figure 1).

Three hypotheses

The first hypothesis is referred to as the late-combination hypothesis (see Figure 1a). This hypothesis stipulates that piloting and path integration generate independent goal estimates, and these two estimates are combined to produce the final goal estimate. This hypothesis is similar to the homing hypothesis described in Zhang et al. (2020), which stipulated that piloting and path integration generate independent home estimates (e.g., Chen et al., 2017). Path integration updates self-to-object (self-to-goal) vectors, whereas piloting updates inter-object (landmark-to-goal) vectors (Benhamou et al., 1990; Etienne & Jeffery, 2004; He & McNamara, 2018; Hodgson & Waller, 2006; Lu et al., 2020; Mou et al., 2004; Wang & Spelke, 2002; Wiener et al., 2011). Consequently, path integration and piloting independently generate their own estimates of a goal vector. These two separate goal estimates are then combined to form a final goal estimate. Thus, the cue combination of path integration and piloting only occurs in estimating goal locations.

The findings of cue interaction in self-localisation but not in homing reported by Zhang et al. (2020) might not undermine the late-combination hypothesis. We do not have clear reasons to believe that cue interaction in goal-localisation should be the same as in homing. In addition, the findings of no cue combination in homing reported by Zhang et al. might be exceptional and need to be replicated as several other studies reported cue combination in homing (Chen et al., 2017; Newman & McNamara, 2020; Sjolund et al., 2018).

The second hypothesis (see Figure 1b) is referred to as the early-combination hypothesis. Zhang et al. (2020) proposed the self-localisation hypothesis to explain homing behaviours, stipulating that cue interaction occurs in self-localisation rather than homing. The early-combination hypothesis is the extension of the self-localisation hypothesis to goal-localisation behaviours, assuming cue interaction is the same in goal-localisation and homing behaviours. According to this hypothesis, path integration and piloting independently generate their own estimates of self-location (including both position and heading estimates) but not two separate goal estimates. These self-location estimates are combined (i.e., position estimates and heading estimates are combined, respectively) prior to goal-localisation. Navigators pinpoint their combined self-location estimates (combined position estimates and combined

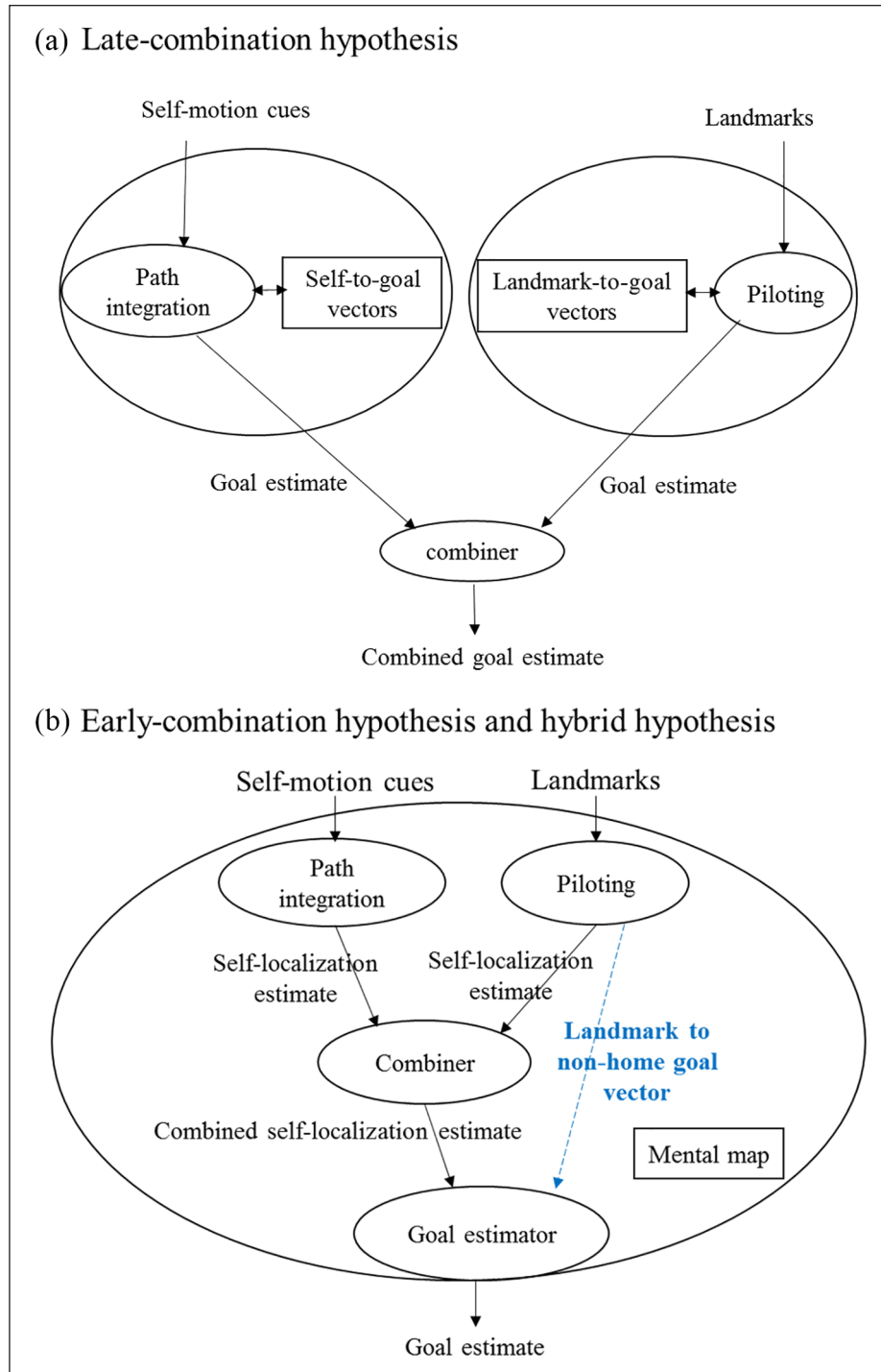


Figure 1. (a) Late-combination hypothesis. (b) Early-combination hypothesis (excluding the dashed line) and dual-combination hypothesis (including the dashed line). Self-localisation estimates include position and heading estimates; combiners include those for position estimates and heading estimates (Zhang et al., 2020). The dual-combination hypothesis claims cue combination in goal-localisation (illustrated by the dashed line) as well as in self-localisation, whereas the early-combination hypothesis claims cue combination only in self-localisation.

heading estimates) in the mental map and then determine the locations of goals. Thus, the cue combination of path integration and piloting only occurs in estimating self-location.

The third hypothesis (the dual-combination hypothesis) is derived from the early-combination hypothesis but with important differences. Same as the early-combination hypothesis, the dual-combination hypothesis stipulates

that the cue combination occurs in the self-localisation; the combined self-localisation is used to calculate the goal location (including home and non-home goals). However, different from the early-combination hypothesis, the dual-combination hypothesis contains a representation of the vector between landmarks and non-home goals (see the dashed line in Figure 1b). This vector is combined with the goal location estimate based on the combined self-localisation, producing the final goal location estimate.

The dual-combination hypothesis distinguishes between homing and non-home goal-localisation regarding cue interaction. Cue interaction in homing and non-home goal-localisation might differ for the following reasons. First, a path home is the starting location of the path, and participants' testing position is usually the ending location of the outbound path (e.g., Nardini et al., 2008). The same path strongly links the home location and participants' testing position (home and self-location). In contrast, non-home goals are usually not located on the path. As a consequence, the path cannot associate goal location with self-location. Second, people may depart from different places, but the desired goal locations remain stable in the environment. Considering these differences, it tends to be efficient to encode the home location relative to the navigator but encode the non-home goal location relative to fixed reference points (landmarks) in the environment.

There is indirect evidence supporting that cue interaction in homing and non-home goal-localisation might differ. In contrast to the findings of no cue combination in homing (Zhang et al., 2020), Mou and Spetch (2013) demonstrated that participants combined estimates of a target location based on another object and based on their own body. Mou and Spetch did not directly examine cue combination between path integration and piloting during navigation as participants did not locomote throughout their experiments. Nevertheless, it is possible that participants can directly use an external landmark location to estimate a (non-home) goal location even when locomotion is involved. Thus, cue combination occurs in both self-localisation and goal-localisation for non-home goals, whereas cue combination may only occur in self-localisation for homing.

Present project

General methods. All experiments were conducted in immersive virtual environments. Participants completed a goal-oriented navigation task. Specifically, they learned the locations of three goals (i.e., one at home and two non-home goals) with the presence of landmarks and then walked two-leg paths (see Figure 2, in the order of leg OT and leg TP) without seeing goals and landmarks. After walking, participants indicated the goals' locations under four cue conditions (Path-Integration, Landmark, Both, and Conflict) (Chen et al., 2017; Nardini et al., 2008; Sjolund et al., 2018; Zhang et al., 2020; Zhao & Warren, 2015).

Zhang et al. (2020) developed a mathematical model, conjecturing that the length ratio (PT/TO, Figure 2) modulates how the combined self-localisation estimates determine the appearance or disappearance of the cue combination for homing estimates. Their model is based on two premises. One premise states that the larger the length ratio of the path, the heavier the navigators' position errors from path integration would depend on the heading errors from path integration (i.e., if you misunderstand your walking direction, the error of your estimate of your position relative to the starting location will increase with the walking distance; see equation (6) in Zhang et al.). The other premise states that the heading and position estimates jointly contribute to homing estimates (see equation (5) in Zhang et al.). Following the model, Zhang et al. ran a simulation showing that cue combination in heading estimates will lead to the appearance of cue combination in homing when the length ratio (PT/TO) is small but not when the length ratio is large. For the interests of brevity, we will briefly summarise their main ideas below and provide a more detailed description in section "General discussion."

Zhang et al. (2020) stated that when the length ratio (PT/TO) is large, the highly correlated position and heading errors from path integration cancel each other in contributing to the homing error, leading to a small homing error. Because position estimates from path integration are independent of the heading estimates from landmarks, the dependency between the heading and position estimates decreases as people assign more weights to the landmarks in averaging the heading estimates from path integration and landmarks. Thus, a large landmark weight in heading estimation might lead to a large homing error (due to decreased dependency and cancel-out). Therefore, the landmark weight that could lead to the appearance of variance reduction for homing errors should be small. However, when landmarks provide more precise heading estimates than does path integration, people use a large landmark weight. Consequently, it is less likely to witness the variance reduction for the homing errors when people combine cues for heading estimates, especially for a large length ratio (PT/TO). The empirical findings of their study confirmed this prediction, showing the appearance of the cue combination in homing when the length ratio is small (length ratio=0.5) and the disappearance of the cue combination in homing when the length ratio is large (length ratio=2).

Note that the two premises of Zhang et al.'s model are still valid, extending from homing (O) to goal-localisation (G) in the current study (see Supplementary Materials for details). Hence, similar to the manipulation of the length ratio (PT/TO), the current study manipulated the length ratio PT/TG (G replacing O) across different goals within each trial (each path). For each trial of each cue condition, we simultaneously obtained heading error, position error, and goal error for each goal (see more details in the data analysis of Experiment 1).

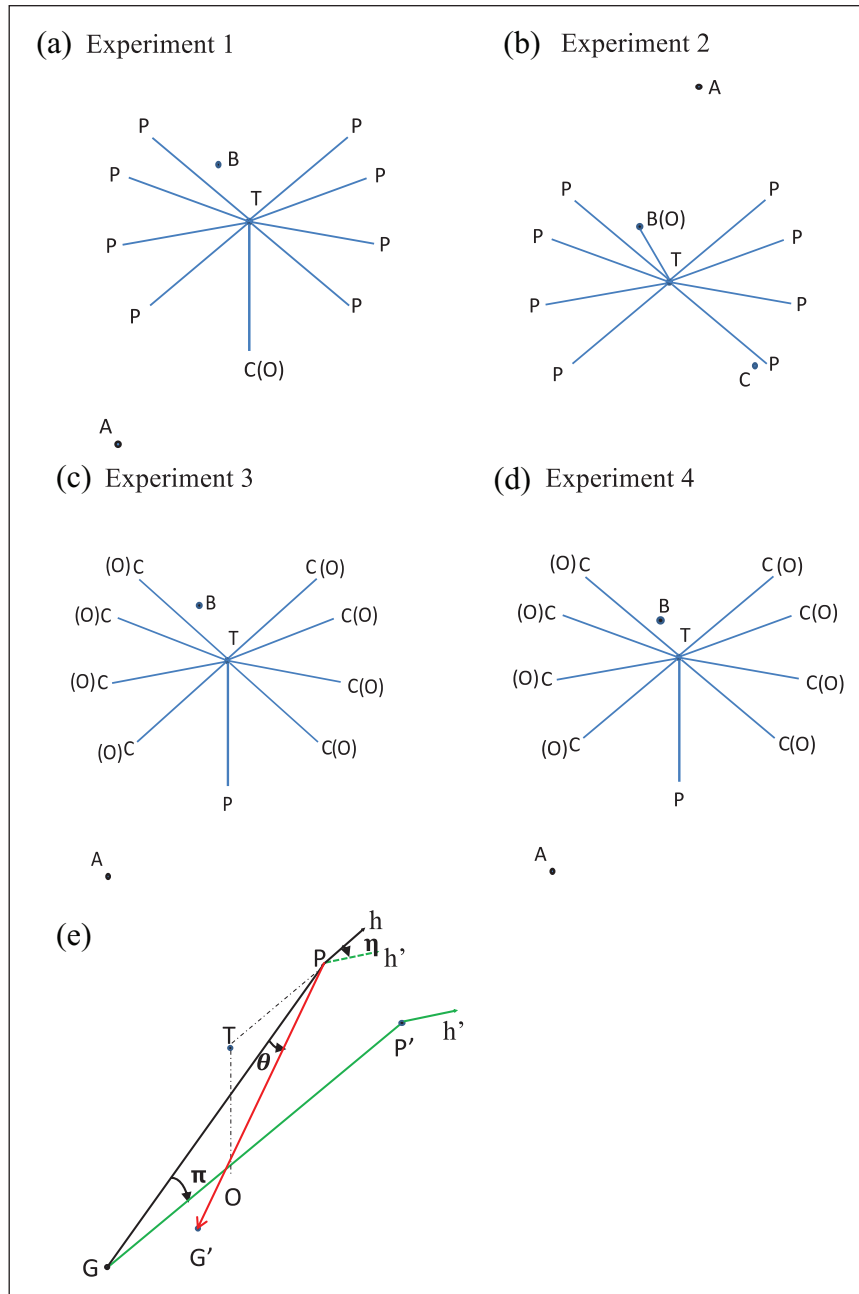


Figure 2. Schematic illustration of path configurations and angular errors calculated in experiments. (a–d) The array of the three objects and eight walking paths (solid lines) used in Experiments 1, 2, 3, and 4, respectively. Each O indicates a path origin. Each P indicates one possible testing position at the end of the second leg. Each A, B, and C in the figures indicate the locations of Goal A, Goal B, and Goal C, respectively. (e) Example of the angular errors for heading, position, and goal estimates (η , π , and θ , respectively). Participants' estimates of their testing position and heading (P and h) are P' and h'. Goal angular error (θ) is the angle from (PG) to (PG'). Position angular error (π) is the angle from (GP) to (GP'). Heading error (η) is the angle from the direction h to direction h'.

The three hypotheses have different predictions on the roles of the length ratio and the goal type (home vs. non-home goals) in cue combination for goal estimates. As illustrated in Table 1, the late-combination hypothesis predicts that cue combination occurs in goal estimates regardless of the length ratio and regardless of goal type. The

early-combination hypothesis predicts that cue combination for goal estimates appears for the small length ratio but not for the large length ratio. This prediction holds regardless of the goal type.

The predictions of the dual-combination hypothesis are not distinct from those of the early-combination

Table 1. The predictions of the three hypotheses on the roles of length ratio and goal type (home vs. non-home goals) in cue combination for goal-localisation (when distal landmarks cannot or when proximal landmarks can specify the goal locations).

Landmark	Length ratio	Late-combination hypothesis		Early-combination hypothesis		Dual-combination hypothesis	
		Home	Non-home goal	Home	Non-home goal	Home	Non-home goal
Distal	Small	Yes		Yes		Yes	
	Medium			Uncertain		Uncertain	
	Large			No		No	
Proximal	Small	Yes		Yes		Yes	Yes
	Medium			Uncertain		Uncertain	Yes
	Large			No		No	Yes
	Very large			No		No	No

Note. Yes: the appearance of cue combination; No: the absence of cue combination; Uncertain: not certain of the results. In experiments, we used small length ratio=0.5, medium=1, large=2, and very large=3. The smallest length ratios to observe no cue combination predicted by each hypothesis are highlighted in gray. The predictions on home alone were systemically tested in Zhang et al. (2020) and were not the primary focus of the current study. Thus, the current study used the medium and large length ratios for distal landmarks and the medium length ratio for proximal landmarks to replicate no combination for homing. The results indicated that the medium length ratio was sufficient to show no combination for homing.

hypothesis when the landmarks are distal and unable to indicate the goal locations (Doeller & Burgess, 2008). However, the dual-combination hypothesis claims that combined self-localisation and the proximal landmarks produce separate estimates for non-home goals (Buckley et al., 2015), whereas only the combined self-localisation produces homing estimates. Consequently, the dual-combination hypothesis predicts different cue combination results for non-home goals and for homing when proximal landmarks, which can indicate the goal locations, are available. Although cue combination for homing should not occur for the large length ratio (length ratio=2) as shown by Zhang et al. (2020), cue combination for non-home goals may appear for the large length ratio because of the landmark to non-home goal vectors (see elaborate explanations in section “General discussion”). To observe no cue combination for a non-home goal, an even larger length ratio (e.g., length ratio=3) might be required.

In addition, whereas the late-combination hypothesis predicts no cue combination for self-localisation, the other two hypotheses predict cue combination for self-localisation (heading and position estimates) as reported by Zhang et al. (2020).

Following Zhang et al. (2020), we qualified the cue combination using two criteria illustrated in Table 2. Cue combination was supported only if both criteria were met. As the three hypotheses differ regarding the stage of cue interaction (in self-localisation vs. in goal-localisation) rather than the format of cue interaction (cue combination vs. cue competition), cue combination in the current study includes the case in which people only rely on the more precise cue when one cue is much more precise than the other (Zhang et al., 2020). Thus, variance reduction is determined by a smaller estimate variance when both cues are available than when only the less precise cue is available (Butler et al., 2010, equation (9)).

Table 2. The two criteria to test a cue combination model.

Criterion	Testing equations
Variance reduction	$\sigma_{12}^2 \leq \min(\sigma_1^2, \sigma_2^2)$
Minimum variance	$W_{1optimal} = \frac{\sigma_2^2}{\sigma_1^2 + \sigma_2^2}$ $\sigma_{12optimal}^2 = \frac{\sigma_1^2 \times \sigma_2^2}{\sigma_1^2 + \sigma_2^2}$

Note. Both criteria should be met to obtain cue combination. σ_1^2, σ_2^2 is the estimate variance using Cue 1 and Cue 2, respectively. σ_{12}^2 is the estimate variance using both Cue 1 and Cue 2. $W_{1optimal}$ is the weight of the estimate based on Cue 1 in a linear combination of two estimates^a ($E_{12} = W_1 \times E_1 + W_2 \times E_2$) that leads to the minimum variance of the combined estimate ($\sigma_{12optimal}^2$).

^aThe estimates derived from Cue 1 and Cue 2, respectively (i.e., E_1 and E_2 , respectively) are linearly combined: $E_{12} = W_1 \times E_1 + W_2 \times E_2$ where E_{12} is the combined estimate when both the two-cues are available and W_1 and W_2 are the weights assigned to Cue 1 and Cue 2, respectively.

The Both and Conflict conditions were two-cue conditions. The Conflict condition can additionally provide the relative weights of the self-motion cues and landmark cues as the two-cues indicated inconsistent value on some metric parameters (e.g., orientation) (Nardini et al., 2008; Rouder et al., 2009). However, in the Conflict condition, due to individual differences (e.g., the ability to detect the variability of visual cues), some participants may notice the shift of visual landmarks in some trials and utilise different strategies from trial to trial, impairing the informativeness of the response variability for the Conflict condition (Sjolund et al., 2018). Thus, the results of the Both condition are primarily considered to examine the appearance of cue combination in terms of variability in the current study.

We conducted four experiments. Experiments 1 and 2 tested these hypotheses when only distal landmarks were available. The distal landmarks were placed far from

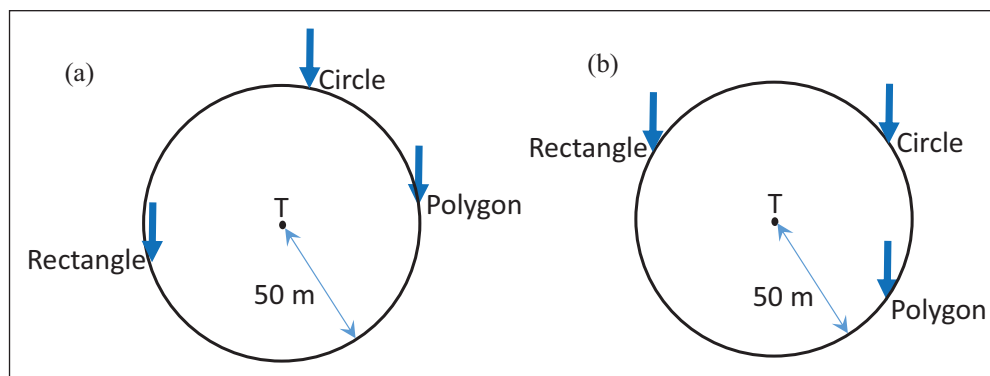


Figure 3. Schematic illustration of the virtual environment in experiments from a top view. T is the turning point of the outbound path. (a) The landmarks (a circle, polygon, and rectangle) attached to the wall. (b) The rotated clockwise landmarks in the Conflict condition.

participants such that landmarks only indicated orientations but not locations. Using distal landmarks, which cannot alone influence goal-localisation, Experiments 1 and 2 could not distinguish between the early-combination hypothesis and the dual-combination hypothesis. Therefore, these two experiments primarily distinguished between the late-combination hypothesis and the other two hypotheses. Experiments 3 and 4 tested these hypotheses when proximal landmarks were available. Proximal landmarks alone could directly indicate goal locations. Consequently, Experiments 3 and 4 primarily distinguished between the early-combination hypothesis and the dual-combination hypothesis.

Experiment 1

Experiment 1 distinguished between the late-combination hypothesis and the other two hypotheses using distal landmarks. In an immersive virtual environment, participants, standing at the path origin (O in Figure 2), learned the locations of three goal objects (Goals A, B, and C) in the presence of distal landmarks. Object C was placed at the path origin ($C=O$). Participants then walked a two-leg path (C-T-P) without the view of landmarks and goals. At the end of each path (P), participants placed goals back in one of four cue conditions. Three locations of the goal objects (G) correspond to different length ratios of PT/TG (i.e., $PT/TA=0.5$, $PT/TC=1$, and $PT/TB=2$). The late-combination hypothesis predicts the cue combination for estimating goal locations in all length ratios and no cue combination for heading estimates. Both the early-combination and dual-combination hypotheses predict the appearance of cue combination for estimating goal locations in a small length ratio ($PT/TA=0.5$) but not in a large length ratio ($PT/TB=2$). This experiment cannot distinguish between the early-combination hypothesis and the dual-combination hypothesis because distal landmarks cannot alone directly influence goal-localisation. Cue combination for position estimates is not relevant to differentiating these three hypotheses because the position

estimates in all cue conditions are from path integration (Zhang et al., 2020).

Method

Participants. Twenty-eight people (14 men and 14 women, aged 18–27 years) participated in the experiment to fulfil a partial requirement for an introductory psychology course. In this and subsequent experiments, the procedure was approved by the University of Alberta Research Ethics Board, and written consent was obtained from each participant before experiments. We used the same number of participants as in Zhang et al. (2020) which showed a large effect size (Cohen's $d=1.0$) and sufficient power (.95) in testing the minimum variance of the homing error (see the $L2/L1=2$ group in Experiment 1 of Zhang et al., 2020).

Materials and design. The experiment was conducted in a physical room of $4 \times 4 \text{ m}^2$. A virtual environment with an endless grassy plane was generated using the Vizard software (WorldViz, Santa Barbara, California) and displayed using a head-mounted display (HMD, Oculus Rift, refresh rate of 90 Hz). The HMD had a diagonal 110° field-of-view and $1,080 \times 1,200$ pixels. Participants' head position and orientation were tracked with an InterSense IS-900 motion tracking system (InterSense, Inc., Massachusetts; sampling rate of 180 Hz). Thus, participants could physically move the location and orientation of their heads to change view-points in the virtual environment. The distal landmarks were three shapes (a circle, rectangle, and polygon) on a huge circular wall with a radius of 50 m and a height of 10 m (Figure 3). Participants held a wand, which was connected to an InterSense IS-900 sensor, to control a virtual stick. As a result, they could use the virtual stick to point to positions and replace objects in the virtual environment.

The outbound walking paths shared the same origin (O in Figure 2a) and turning point (T) but differed in the ending position (P). The lengths of two legs for the outbound path were 1.8 m (i.e., $TO=1.8 \text{ m}$ and $PT=1.8 \text{ m}$). The

turning point of the path (T in Figure 2a) was always at the centre of the physical room. The turning angle could be 50°, 80°, 100° or 130° clockwise or counterclockwise, forming eight paths. To guide participants to walk each path, a sequence of three poles indicated the origin (O), the turning position (T), and the ending position (P). The poles were 2 m in height and 0.05 m in radius, red for the first two positions (O and T) and green for the last position (P). Once participants reached the poles, the poles disappeared.

There were three goal locations. One goal location was the origin (C=O in Figure 2a). The other two goal locations (A and B in Figure 2a) were located 3.6 and 0.8 m from the turning point in the directions of 210° and 330° clockwise, relative to the direction of the first leg, respectively. The three goal locations created three length ratios (PT/TG=2, 1, and 0.5). Specifically, PT/TB=2 as the PT was 1.8 m and the TB was 0.9 m, PT/TC=1 as both PT and TC were 1.8 m, and PT/TA=0.5 as the PT was 1.8 m and the TA was 3.6 m. Three common objects (a clock, mug, and scissors) were used as goal objects. The object–location pair was randomised across participants but was consistent across trials for each participant.

The four cue conditions were distinguished after participants reached the end of the outbound path (P). In the Path-Integration condition, the visual landmarks (i.e., shapes) were absent so participants had to rely solely on path integration in goal-localisation. In the Landmark condition, the shapes reappeared after participants were disoriented at the end of the path. In the Both condition, participants saw the reappeared shapes without being disoriented. The Conflict condition was the same as the Both condition, except that the shapes (i.e., the landmarks) were rotated covertly by 45° clockwise or counterclockwise so that the correct direction indicated by landmarks was inconsistent with the one indicated by self-motion cues. The rotation direction was clockwise (shown in Figure 3b) for half of the participants. We used a rotation of 45° as in Zhang et al. (2020).

All 28 participants completed the eight paths in each of the four cue conditions. The 32 trials in total were in a random order for each participant.

Procedure. Before the experimental trials, the participants completed four practice trials displayed in a predetermined order (Both, Path-Integration, Landmark, Conflict) to familiarise themselves with the procedure. The experimental trials are similar to practise trials but use different objects and different paths. There were a learning phase and a testing phase for each trial. Each trial started by presenting a red pole to indicate the origin. After participants reached the origin, the first pole disappeared, and a second red pole was presented at T to establish the learning orientation. After participants faced the second pole, the learning phase of this trial started.

In the learning phase, participants saw the shapes on the wall and the three goal objects on the ground. They learned the directions of the shapes and the locations of the objects

(for 3 min in the first trial and 30 s in the remaining 31 trials). Afterwards, participants used the virtual stick to indicate the original locations of objects and the original directions of shapes, while objects and shapes disappeared. Each object and landmark were probed in random order. Feedback on presenting the probed object or shape in the correct location appeared after participants' responses to each probe and disappeared after participants were instructed by the experimenter to see the feedback in practice trials or after 2 s in experimental trials, respectively. Such replacing and feedback occurred for two rounds in the first trial and one round in the following 31 trials, given that the object–relation pairs were consistent across trials for each participant.

After studying at O, the participants walked towards the red pole appearing at T without viewing the objects. When they arrived at the red pole (at T), the pole and the shapes on the wall were removed (the bare wall was not removed). A green pole at the testing position showed up and guided the participants to walk towards it. Once the participants reached the pole, it disappeared. The procedure was the same for all four conditions. This procedure that only the self-motion cue can be accessed along the outbound path was consistent with Zhang et al. (2020) but departed from some cue combination studies (Chen et al., 2017) in which both the self-motion and landmark cues existed on the outbound path. However, it had been confirmed that the number of cues available on the outbound path had a negligible influence on measuring cue combination during navigation (Newman & McNamara, 2020).

Then the testing phase started. In the Path-Integration, Both, and Conflict conditions, the participants engaged in a counting task for 8 s while they stood at P. In the Landmark condition, the participants spun clockwise or counterclockwise for 8 s while they were completing the counting task. After 8 s had elapsed, the landmarks (i.e., shapes) reappeared in the Landmark, Both, and Conflict conditions. Participants were required to use the virtual stick to indicate the locations for all three goals probed in random order. No feedback was presented. After the testing phase, all visual items in the virtual environment except the endless grassy plane were removed and the participants were led by the experimenter to a random location in the physical room. A red pole was placed at the origin to start the next trial.

Data analysis. Following Zhang et al. (2020), the participants' estimated self-location (P' and h') for each trial (path) was obtained employing the methodology of bidimensional regression based on the correspondence between the correct goal locations (A, B, and C) and the responded goal locations (A' , B' , and C'). The assumption is that the relationship between the remembered locations of objects (A, B, and C) and the estimated self-location (P' and h') was analogous to the relationship between their replacing objects (A' , B' , and C') and their actual self-location (P and h). In other words, participants based on the

spatial relations between their estimated locations and objects' locations in their mental maps to replace the objects (Fujita et al., 1993). Specifically, for each trial of each cue condition, we obtained the mapping function (i.e., f) between the original and remembered locations of three objects (goals) using the bidimensional regression, $G=f(G')$ (Friedman & Kohler, 2003). We then calculated participants' estimates of their position and heading (i.e., self-localisation) using the mapping function (f) and participants' testing position and heading, $P'=f(P)$, $h'=f(h)$. The mean r^2 for the regression models across paths and participants was larger than .85 in all experiments of the current study, reflecting that participants responded coherently across objects within individual paths

Using the estimated position (P') and heading (h'), we calculated the angular errors for all heading, position, and goal estimates (η , π , and θ ; see an example in Figure 2e). In each trial, there was only one heading angular error, three position angular errors as the bearing of participants' position (either correct or estimated one) can be specified relative to each goal location, and three goal angular errors (one for each goal).

For the participants who experienced the clockwise shift of the landmarks in the Conflict condition, the sign of the individual angular error (i.e., heading error, position error, and goal error) was flipped. Consequently, the predicted heading error (η) and goal error (θ) indicated by the rotated distal landmarks, all in the counterclockwise direction now, would be 45° and -45° , respectively (clockwise is positive in the current project). For the circular mean of errors across paths for each participant, the closer the value is to 0, the less bias of individual's estimation is towards rotated landmarks in the Conflict condition.

We calculated the observed weight assigned to the landmark cue ($W_{observed} = E_{observed} / E_{predicted}$) in the heading or goal estimates in the Conflict condition for each participant. $E_{observed}$ denotes the observed estimate error and $E_{predicted}$ denotes the estimate error predicted by the landmark cue. $E_{predicted}$ was 45° for heading error and -45° for goal errors, respectively.

Across trials, we calculated the estimation variability in each cue condition. The estimation variability in each cue condition was the circular standard deviation, SD , of errors across paths. Cue combination analyses for position errors are not applicable because the position error was only generated theoretically from path integration in all cue conditions (Zhang et al., 2020). Furthermore, Bayesian Factor (BF_{01}) was reported for any non-significant comparison (Rouder et al., 2009).

Results

We report the results of the goal errors and heading errors below. Similar to Zhang et al. (2020), the current study cannot fully test the cue combination for position errors.¹ In addition, the results of the position errors did not

provide any information further than the heading errors. For the interests of brevity, the results of the position errors are reported in Supplementary Materials. The circular means of errors across participants are also reported in Supplementary Materials to indicate the estimation bias in the Conflict condition.

Goal errors. The mean SD s of goal errors in the four cue conditions and the mean optimal SD s are presented in Figure 4. We tested a cue combination using both variance reduction and minimum variance (see Table 2 for testing equations).

A two-way repeated-measures analysis of variance (ANOVA) with cue condition (Path-Integration, Landmark, Both, Conflict) and length ratio of goals (PT/TG=2, 1, 0.5) as independent variables revealed a significant interaction between the cue condition and length ratio of goals, $F(6, 162)=4.68, p < .001, MSE=181.27, \eta_p^2 = .15$. Due to the significant interaction, we analysed the different goals in separate one-way repeated measure ANOVAs with cue condition as the independent variable.

For Goal B (PT/TB=2) Overall, there was no variance reduction or minimum variance for either condition of two-cues (Both and Conflict).

In particular, there was no significant main effect of the cue condition, $F(3, 81)=1.08, p = .36, MSE=261.86, \eta_p^2 = .04$, indicating no variance reduction for either condition of two-cues (Both and Conflict). The mean SD in the Both condition was significantly larger than the mean optimal SD , $t(27)=6.53, p < .001$, Cohen's $d=1.75$. The mean SD in the Conflict condition was significantly larger than the mean optimal SD , $t(27)=6.91, p < .001$, Cohen's $d=1.85$. The mean observed weight for the landmark (0.61) was consistent with the mean optimal weight (0.40), $t(27)=1.99, p = .06$, Cohen's $d=0.53, BF_{01}=1.14$. These results indicate no minimum variance for either condition of two-cues.

For Goal C (PT/TC=1, the home) Overall there was variance reduction for the Both and Conflict conditions, but no minimum variance was produced for either two-cue condition.

In particular, we found a significant main effect of the cue condition, $F(3, 81)=4.60, p < .01, MSE=319.20, \eta_p^2 = .15$. The mean SD in the Both condition was not significantly different from that in the Path-Integration condition, $t(27)=0.10, p = .92$, Cohen's $d=0.03, BF_{01}=6.82$, but was significantly smaller than that in the Landmark condition, $t(27)=2.41, p = .02$, Cohen's $d=0.64$. The mean SD in the Conflict condition was not significantly different from that in the Path-Integration condition, $t(27)=1.00, p = .33$, Cohen's $d=0.27, BF_{01}=4.26$, but was significantly smaller than that in the Landmark condition, $t(27)=2.28, p = .03$, Cohen's $d=0.61$. These results demonstrate variance reduction for the Both and Conflict conditions.

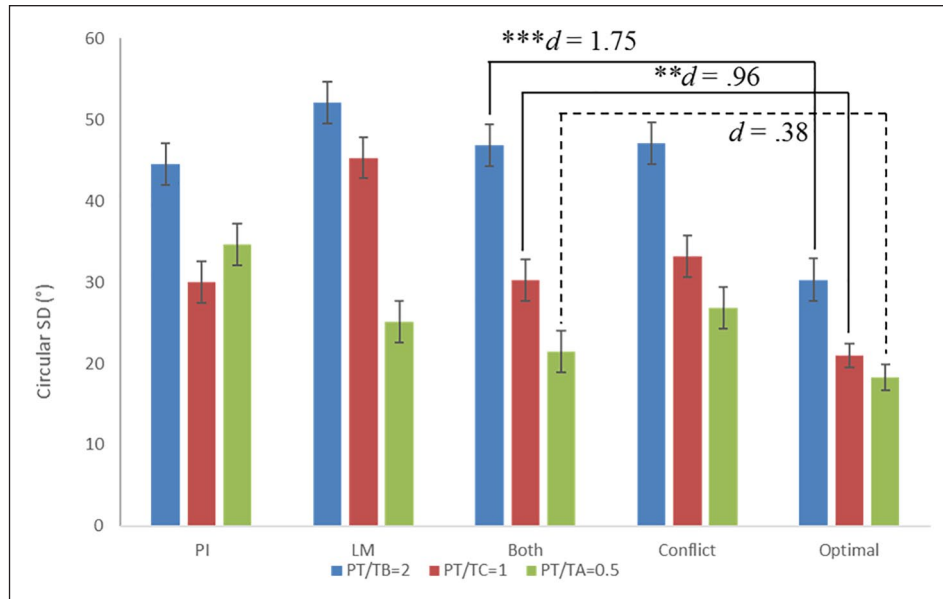


Figure 4. Mean observed SDs of the goal errors (θ) in the Path-Integration (PI), Landmark (LM), Both, and Conflict conditions and the optimal prediction (Optimal) when the length ratio equals 2, 1 (home), and 0.5 in Experiment 1. The solid line means a significant difference (** $p < .01$; *** $p < .001$) and the dashed line means no significant difference. Error bars represent \pm SE of the mean without removing individual differences.

The mean *SD* in the Both condition was significantly larger than the mean optimal *SD*, $t(27)=3.59$, $p=.001$, Cohen's $d=0.96$. The mean *SD* in the Conflict condition was significantly larger than the mean optimal *SD*, $t(27)=4.55$, $p < .001$, Cohen's $d=1.21$. The mean observed weight for the landmark (0.42) was consistent with the mean optimal weight (0.36), $t(27)=0.74$, $p=.47$, Cohen's $d=0.20$, $BF_{01}=5.28$. These results indicate that no minimum variance was produced for either two-cue condition.

For Goal A (PT/TA=0.5) Overall, we found variance reduction for the Both and Conflict conditions and the minimum variance for the Both condition but not for the Conflict condition.

In particular, there was a significant main effect of the cue condition, $F(3, 81)=6.42$, $p=.001$, $MSE=135.12$, $\eta_p^2=.19$. The Both condition had significantly smaller mean *SD* than the Path-Integration condition, $t(27)=4.04$, $p < .001$, Cohen's $d=1.08$, but did not differ significantly from the Landmark condition, $t(27)=1.15$, $p=.26$, Cohen's $d=0.31$, $BF_{01}=3.65$. The Conflict condition had significantly smaller mean *SD* than the Path-Integration condition, $t(27)=2.75$, $p=.01$, Cohen's $d=0.73$, but did not differ significantly from the Landmark condition, $t(27)=0.48$, $p=.63$, Cohen's $d=0.13$, $BF_{01}=6.12$. These results indicate variance reduction for the Both and Conflict conditions.

The mean *SD* in the Both condition was consistent with the mean optimal *SD*, $t(27)=1.42$, $p=.17$, Cohen's $d=0.38$, $BF_{01}=2.68$. The mean *SD* in the Conflict condition was significantly larger than the mean optimal *SD*, $t(27)=3.56$, $p=.001$, Cohen's $d=0.95$. The mean observed weight for

the landmark (0.66) was not significantly different from the mean optimal weight (0.65), $t(27)=.23$, $p=.82$, Cohen's $d=0.06$, $BF_{01}=6.68$. These results indicate that the minimum variance was produced for the Both condition but not for the Conflict condition.

Heading errors. The mean *SDs* of heading errors in the four cue conditions as well as the mean optimal *SD* are illustrated in Figure 5. A repeated-measures ANOVA was conducted to analyse the cue effect on heading errors.

Overall, we found both variance reduction and minimum variance for the Both condition. We also found variance reduction but no minimum variance for the Conflict condition.

In particular, there was a significant main effect of the cue condition, $F(3, 81)=17.76$, $p < .001$, $MSE=153.13$, $\eta_p^2=.40$. The mean *SD* in the Both condition was significantly smaller than that in the Path-Integration condition, $t(27)=5.29$, $p < .001$, Cohen's $d=1.41$, but was not significantly different from that in the Landmark condition, $t(27)=1.02$, $p=.32$, Cohen's $d=0.27$, $BF_{01}=4.16$. The mean *SD* in the Conflict condition was significantly smaller than that in the Path-Integration condition, $t(27)=4.79$, $p < .001$, Cohen's $d=1.28$, but was not significantly different from that in the Landmark condition, $t(27)=.01$, $p=.99$, Cohen's $d < 0.01$, $BF_{01}=6.85$. These results indicate variance reduction for the Both and Conflict conditions.

The mean *SD* in the Both condition was consistent with the mean optimal *SD*, $t(27)=0.87$, $p=.39$, Cohen's $d=0.23$, $BF_{01}=4.76$. The mean *SD* in the Conflict condition was

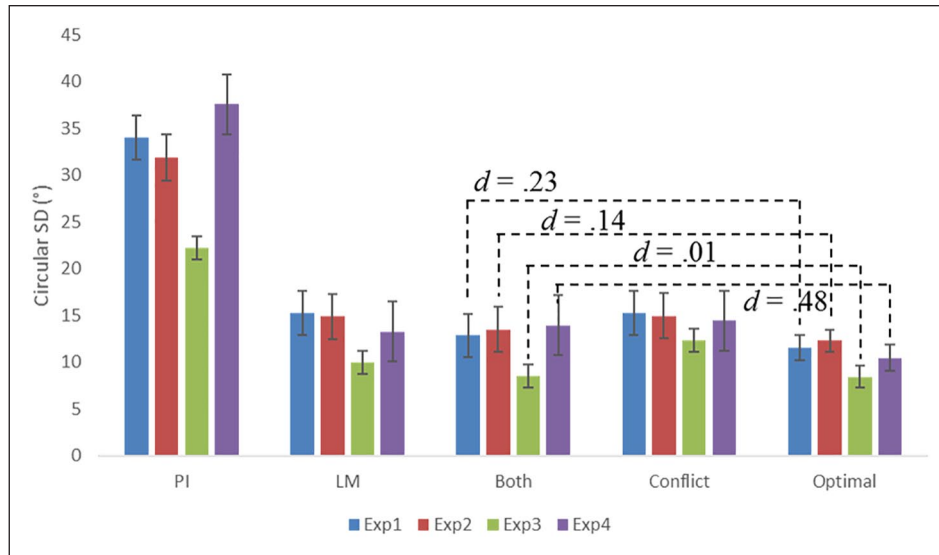


Figure 5. Mean observed SDs of the heading errors (η) in the Path-Integration (PI), Landmark (LM), Both, and Conflict conditions and the optimal prediction (Optimal) in all experiments. The dashed line means no significant difference. Error bars represent $\pm SE$ of the mean without removing individual differences.

significantly larger than the mean optimal SD, $t(27)=2.60$, $p=.02$, Cohen's $d=0.70$. The mean observed weight for the landmark (0.71) did not significantly differ from the mean optimal weight (0.76), $t(27)=0.80$, $p=.43$, Cohen's $d=0.21$, $BF_{01}=5.03$. These results show that the minimum variance was generated for the Both condition but not for the Conflict condition.

Discussion

The results of Experiment 1 showed a cue combination (i.e., variance reduction and minimum variance, see the definitions in Table 2) for heading estimates in the Both condition, albeit not in the Conflict condition. Furthermore, the cue combination for goal estimates only occurred for the length ratio of 0.5 in the Both condition but neither for the other two larger ratios (i.e., 1, 2) in the Both condition nor for all three length ratios in the Conflict condition. Overall, these results favoured the early-combination hypothesis and the dual-combination hypothesis over the late-combination hypotheses. The no cue combination for heading estimates in the Conflict condition might be because some participants may notice the shift of visual landmarks in some trials (Sjolund et al., 2018). To ensure that the findings of Experiment 1 were reliable, we conducted Experiment 2 with some changes in the goal locations.

Experiment 2

In Experiment 2 (see Figure 2b), we sought to replicate the findings of Experiment 1 after changing the starting location of the paths and using different goal locations. In particular, although the length ratios for all three goals were still about 0.5 (0.6 exactly), 1, and 2, the length ratio (PT/TG) for the

home changed from 1 in the previous experiment to 2 in the current experiment. Accordingly, one of the non-home goals changed from 2 in the previous experiment to 1 in the current experiment.

Method

Participants. Twenty-eight people (14 men and 14 women, aged 18–39 years) participated in the experiment to fulfil a partial requirement for an introductory psychology course.

Materials, design, and procedure. Experiment 2 was similar to Experiment 1 except for the following changes. First, Goal A and Goal C were placed at different locations but kept their approximate corresponding length ratios. Second, the origin of the walking path was switched to Goal B in the current experiment so that the length ratio for the home equalled 2.

Results

Goal errors. The mean SDs of goal errors in the four cue conditions and the mean optimal SDs are presented in Figure 6. A two-way repeated-measures ANOVA with cue condition (Path-Integration, Landmark, Both, Conflict) and length ratio of goals (2, 1, 0.6) as independent variables revealed a significant interaction between the cue condition and length ratio of goals, $F(6, 162)=3.98$, $p=.001$, $MSE=153.16$, $\eta_p^2=.13$. Due to the significant interaction, we analysed the different goals in separate one-way ANOVAs with cue condition as the independent variable.

For Goal B (PT/TB=2, the home) Overall, we found no variance reduction or minimum variance for either two-cue condition.

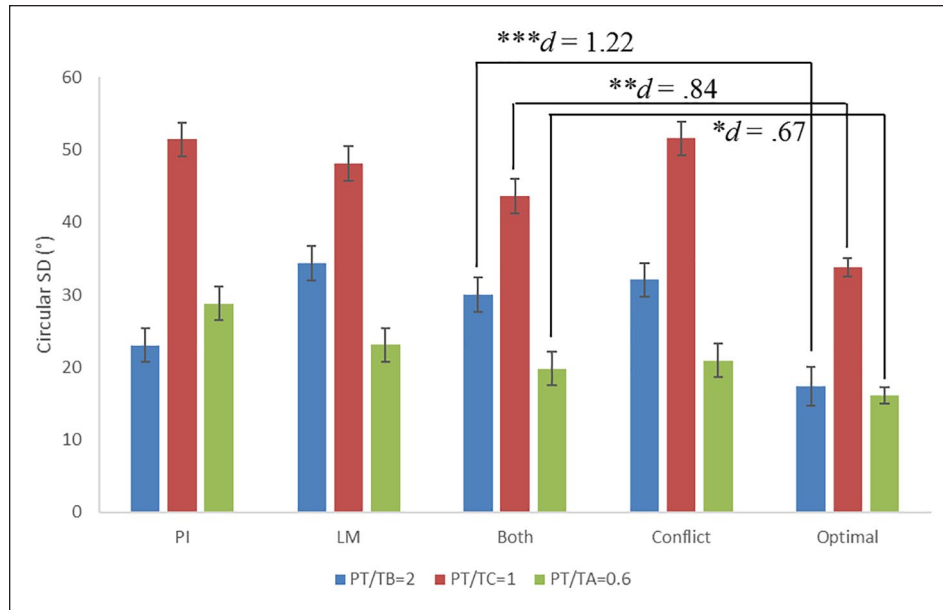


Figure 6. Mean observed SDs of the goal errors (θ) in the Path-Integration (PI), Landmark (LM), Both, and Conflict conditions and the optimal prediction (Optimal) when length ratio equals 2 (home), 1, and 0.6 in Experiment 2. The solid line means a significant difference ($*p < .05$; $**p < .01$; $***p < .001$). Error bars represent $\pm SE$ of the mean without removing individual differences.

In particular, there was a significant main effect of the cue condition, $F(3, 81) = 4.17$, $p < .01$, $MSE = 160.23$, $\eta_p^2 = .13$. The Both and Conflict conditions had significantly larger mean SDs than the Path-Integration condition, $t(27) = 2.15$, $p = .04$, Cohen's $d = 0.58$ and $t(27) = 2.24$, $p = .03$, Cohen's $d = 0.60$, respectively. The mean SDs in the Both and Conflict conditions were not significantly different from the SD in the Landmark condition, $t(27) = 1.5$, $p = .14$, Cohen's $d = 0.40$, $BF_{01} = 2.39$ and $t(27) = .63$, $p = .54$, Cohen's $d = 0.17$, $BF_{01} = 5.67$, respectively. These results indicate no variance reduction for either two-cue condition.

The Both and Conflict conditions had significantly larger mean SDs than the mean optimal SD, $t(27) = 4.55$, $p < .001$, Cohen's $d = 1.22$ and $t(27) = 4.25$, $p < .001$, Cohen's $d = 1.14$, respectively. The mean observed weight for the landmark (0.35) did not significantly differ from the mean optimal weight (0.37), $t(27) = .20$, $p = .84$, Cohen's $d = .05$, $BF_{01} = 6.72$. These results indicate that no minimum variance was achieved for either two-cue condition.

For Goal C (PT/TC=1) Overall, we found no variance reduction or minimum variance for either two-cue condition.

In particular, the effect of the cue condition did not reach significant, $F(3, 81) = 2.03$, $p = .12$, $MSE = 194.03$, $\eta_p^2 = .07$, suggesting no variance reduction for either two-cue condition. The Both and Conflict conditions had significantly larger mean SDs than the mean optimal SD, $t(27) = 3.14$, $p < .01$, Cohen's $d = 0.84$ and $t(27) = 5.17$, $p < .001$, Cohen's $d = 1.38$, respectively. The mean observed weight for the landmark (0.55) was not significantly different from the

mean optimal weight (0.51), $t(27) = 0.28$, $p = .78$, Cohen's $d = 0.08$, $BF_{01} = 6.59$. These results demonstrate no minimum variance for either two-cue condition.

For Goal A (PT/TA=0.6) We found variance reduction for the Both and Conflict conditions but no minimum variance for either two-cue condition.

In particular, there was a significant main effect of the cue condition, $F(3, 81) = 4.52$, $p < .01$, $MSE = 99.37$, $\eta_p^2 = .14$. The Both and Conflict conditions had significantly smaller mean SDs than the Path-Integration condition, $t(27) = 3.51$, $p < .01$, Cohen's $d = 0.94$ and $t(27) = 2.37$, $p = .03$, Cohen's $d = 0.63$, respectively. The mean SDs in the Both and Conflict conditions were not significantly different from the SD in the Landmark condition, $t(27) = 1.64$, $p = .11$, Cohen's $d = 0.44$, $BF_{01} = 1.99$ and $t(27) = .86$, $p = .40$, Cohen's $d = 0.23$, $BF_{01} = 4.82$, respectively. These results indicate variance reduction for the Both and Conflict conditions.

The Both and Conflict conditions had significantly larger mean SDs than the mean optimal SD, $t(27) = 2.50$, $p = .02$, Cohen's $d = 0.67$ and $t(27) = 2.40$, $p = .02$, Cohen's $d = 0.64$, respectively. The mean observed weight for the landmark (0.61) was not significantly different from the mean optimal weight (0.58), $t(27) = .36$, $p = .72$, Cohen's $d = 0.10$, $BF_{01} = 6.43$. These results show that no minimum variance was produced for either two-cue condition.

Heading errors. Overall, we found variance reduction and the minimum variance for the Both and Conflict conditions (Figure 5).

In particular, there was a significant main effect of the cue condition, $F(3, 81) = 12.91$, $p < .001$, $MSE = 165.66$, $\eta_p^2 = .32$. The Both condition had significantly smaller mean SD than the Path-Integration condition, $t(27) = 3.99$, $p < .001$, Cohen's $d = 1.07$, but did not differ significantly from the Landmark condition, $t(27) = 0.54$, $p = .59$, Cohen's $d = 0.15$, $BF_{01} = 5.94$. The mean SD in the Conflict condition was significantly smaller than that in the Path-Integration condition, $t(27) = 3.74$, $p = .001$, Cohen's $d = 1.00$, but was not significantly different from that in the Landmark condition, $t(27) = .02$, $p = .98$, Cohen's $d < 0.01$, $BF_{01} = 6.85$. These results indicate variance reduction for the Both and Conflict conditions.

The mean SD s in the Both and Conflict conditions were consistent with the mean optimal SD , $t(27) = 0.52$, $p = .61$, Cohen's $d = 0.14$, $BF_{01} = 6.03$ and $t(27) = 1.39$, $p = .18$, Cohen's $d = 0.37$, $BF_{01} = 2.76$, respectively. The mean observed weight for the landmark (0.72) was not significantly different from the mean optimal weight (0.73), $t(27) = 0.18$, $p = .86$, Cohen's $d = 0.05$, $BF_{01} = 6.75$. These results show that the minimum variance was generated for the Both and Conflict conditions.

Discussion

Experiment 2 demonstrated a cue combination for heading estimates but no cue combination for goal estimates even with the smallest length ratio in the Both and Conflict conditions. These findings support the early-combination hypothesis and the dual-combination hypothesis over the late-combination hypothesis.

In Experiments 1 and 2, distal landmarks did not indicate the positions of the goals. Hence, these two experiments could not test whether landmarks could directly influence goal-localisation, thus could not differentiate the early-combination hypothesis from the dual-combination hypothesis. Experiments 3 and 4 tackled this issue.

Experiment 3

Experiment 3 aimed to differentiate the dual-combination hypothesis from the early-combination hypothesis by using proximal landmarks instead of distal landmarks. As shown in Figure 2c, the length ratio for the home was 1, for the non-home goals it was 2 (Goal B) or 0.5 (Goal A). The early-combination hypothesis claims that localising both non-home goals and home solely relies on the combined self-localisation estimates. Therefore, when the length ratio was large (i.e., length ratio = 2), the cue combination for goal estimates, regardless of non-home goals or home, disappeared. In contrast, the dual-combination hypothesis claims that localising non-home goals relies on both the combined self-localisation and the proximal landmarks, whereas homing relies on the combined self-localisation alone. Consequently, the cue combination could appear in localising a non-home goal with a large length ratio (length

ratio = 2) (see Goal B in Figure 2c) but disappear in homing for a medium length ratio (length ratio = 1).

Besides, in Experiment 3, we disoriented participants at the starting point (O in Figure 2c) of the outbound path in the Landmark condition. As disoriented navigators were unable to estimate their position properly based on path integration during the movement after disorientation (Mou & Zhang, 2014), disorienting navigators at the starting point can minimise the contribution from path integration to the position estimate in the Landmark condition. Thus, the position estimate from path integration was disrupted substantially and the goal estimate was solely determined by the proximal landmark.

Method

Participants. Twenty-eight people (14 men and 14 women, aged 17–27 years) participated in the experiment to fulfil a partial requirement for an introductory psychology course.

Materials, design, and procedure. The materials, design, and procedure were the same as those in Experiment 1 except for the following changes. First, the landmarks (shapes) were positioned on a much smaller circular wall (5 m radius, 1 m tall) instead of the 50-m radius circular wall in Experiment 1. Therefore, the proximal shapes alone could indicate the locations of goals and participants' positions. Second, consistent with the previous research, we rotated the landmarks around the testing position (Chen et al., 2017; Zhang et al., 2020).² We varied the origin of the path but kept the testing position constant (Figure 2c) across paths. In particular, we specified a testing position other than the origin (O) as the centre of the wall. Third, participants were disoriented while counting at the starting point of the path after the learning phase and before walking the path in the Landmark condition to completely remove path integration cues in the Landmark condition. Accordingly, the bare wall was also removed even during walking on the first leg as the bare wall could have indicated participants' location and orientation in the outbound path.

Results

Goal errors. The mean SD s of goal errors in the four cue conditions and the mean optimal SD s are presented in Figure 7. A two-way repeated-measures ANOVA with cue condition (Path-Integration, Landmark, Both, Conflict) and length ratio of goals (2, 1, 0.5) as independent variables revealed a significant interaction between the cue condition and length ratio of goals, $F(6, 162) = 7.84$, $p < .001$, $MSE = 69.60$, $\eta_p^2 = .23$. Due to the significant interaction, we analysed the different goals in one-way ANOVAs separately with cue condition as the independent variable.

For Goal B (PT/TB = 2) Overall, we found variance reduction for the Both and Conflict conditions and mini-

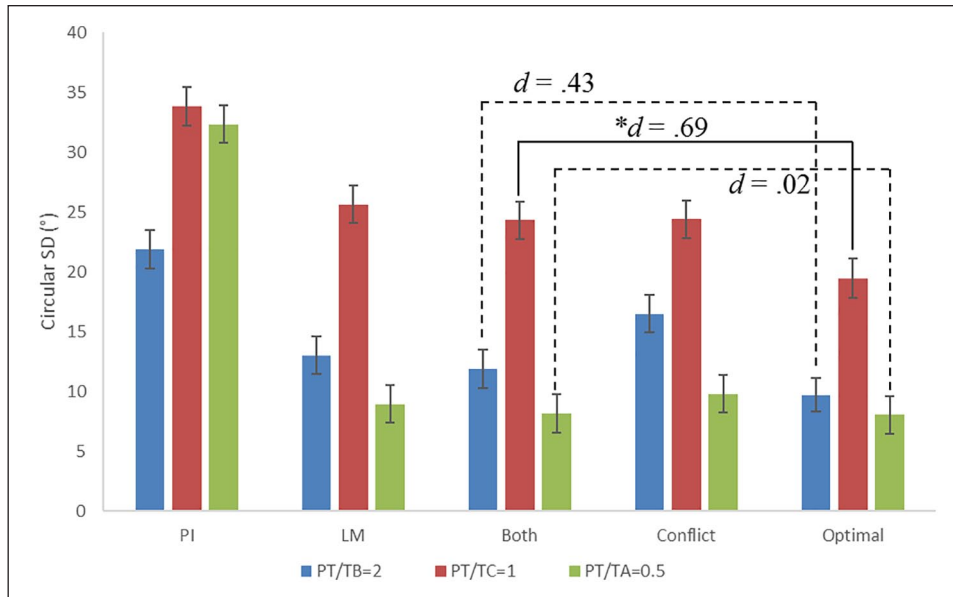


Figure 7. Mean observed SDs of the goal errors (θ) in the Path-Integration (PI), Landmark (LM), Both, and Conflict conditions and the optimal prediction (Optimal) when length ratio is 2, 1 (home), and 0.5 in Experiment 3. The solid line means a significant difference ($*p < .05$) and the dashed line means no significant difference. Error bars represent $\pm SE$ of the mean without removing individual differences.

imum variance for the Both condition but not for the Conflict condition.

In particular, there was a significant main effect of the cue condition, $F(3, 81) = 8.45$, $p < .001$, $MSE = 66.88$, $\eta_p^2 = .24$. The Both condition had significantly smaller mean SD than the Path-Integration condition, $t(27) = 5.49$, $p < .001$, Cohen's $d = 1.47$, but did not differ significantly from the Landmark condition, $t(27) = 0.55$, $p = .59$, Cohen's $d = 0.15$, $BF_{01} = 5.93$. The Conflict condition had significantly smaller mean SD than the Path-Integration condition, $t(27) = 2.01$, $p = .05$, Cohen's $d = 0.54$, but did not differ significantly from the Landmark condition, $t(27) = 1.81$, $p = .08$, Cohen's $d = 0.48$, $BF_{01} = 1.54$. These results demonstrate variance reduction for the Both and Conflict conditions.

The mean SD in the Both condition was consistent with the mean optimal SD, $t(27) = 1.62$, $p = .12$, Cohen's $d = .43$, $BF_{01} = 2.02$. The mean SD in the Conflict condition was significantly larger than the mean optimal SD, $t(27) = 3.88$, $p < .001$, Cohen's $d = 1.04$. The mean observed weight for the landmark (0.86) was significantly larger than the mean optimal weight (0.72), $t(27) = 2.23$, $p = .04$, Cohen's $d = 0.59$. These results indicate that minimum variance was achieved for the Both condition but not for the Conflict condition.

For Goal C (PT/TC = 1, the home) Overall, we found variance reduction for the Both and Conflict conditions but no minimum variance for either two-cue condition.

In particular, there was a significant main effect of the cue condition, $F(3, 81) = 6.33$, $p < .001$, $MSE = 92.23$, $\eta_p^2 = .19$. The Both and Conflict conditions had significantly

smaller mean SDs than the Path-Integration condition, $t(27) = 4.09$, $p < .001$, Cohen's $d = 1.09$ and $t(27) = 3.22$, $p < .01$, Cohen's $d = 0.86$, respectively. The mean SDs in the Both and Conflict conditions were not significantly different from the SD in the Landmark condition, $t(27) = .52$, $p = .61$, Cohen's $d = 0.14$, $BF_{01} = 6.01$ and $t(27) = .52$, $p = .61$, Cohen's $d = 0.14$, $BF_{01} = 6.02$, respectively. These results indicate that variance reduction occurred for the Both and Conflict conditions.

The Both and Conflict conditions had significantly larger mean SDs than the mean optimal SD, $t(27) = 2.57$, $p = .02$, Cohen's $d = 0.69$ and $t(27) = 2.43$, $p = .02$, Cohen's $d = 0.65$, respectively. The mean observed weight for the landmark (0.78) was significantly larger than the mean optimal weight (0.63), $t(27) = 2.30$, $p = .03$, Cohen's $d = .62$. These results indicate that no minimum variance was achieved.

For Goal A (PT/TA = 0.5) We found variance reduction and minimum variance for the Both and Conflict conditions.

In particular, there was a significant main effect of the cue condition, $F(3, 81) = 38.85$, $p < .001$, $MSE = 98.54$, $\eta_p^2 = .59$. The Both and Conflict conditions had significantly smaller mean SDs than the Path-Integration condition, $t(27) = 7.44$, $p < .001$, Cohen's $d = 1.99$ and $t(27) = 6.87$, $p < .001$, Cohen's $d = 1.84$, respectively. The mean SDs in the Both and Conflict conditions were not significantly different from the SD in the Landmark condition, $t(27) = 0.33$, $p = .74$, Cohen's $d = 0.09$, $BF_{01} = 6.50$ and $t(27) = 0.44$, $p = .66$, Cohen's $d = 0.12$, $BF_{01} = 6.24$, respectively. These results indicate that variance reduction occurred for the Both and Conflict conditions.

The mean *SDs* in the Both and Conflict conditions were consistent with the mean optimal *SD*, $t(27)=.06$, $p=.95$, Cohen's $d=0.02$, $BF_{01}=6.84$ and $t(27)=1.01$, $p=.32$, Cohen's $d=0.27$, $BF_{01}=4.19$, respectively. The mean observed weight for the landmark (0.98) was significantly larger than the mean optimal weight (0.89), $t(27)=3.73$, $p=.001$, Cohen's $d=1.00$. These results show that the minimum variance was generated for the Both and Conflict conditions.

Heading errors. Overall, we found variance reduction and minimum variance for the Both condition but not for the Conflict condition (Figure 5).

In particular, there was a significant main effect of the cue condition, $F(3, 81)=25.81$, $p<.001$, $MSE=41.45$, $\eta_p^2=.49$. The Both condition had significantly smaller mean *SD* than the Path-Integration condition, $t(27)=6.86$, $p<.001$, Cohen's $d=1.83$, but did not differ significantly from the Landmark condition, $t(27)=0.92$, $p=.37$, Cohen's $d=0.25$, $BF_{01}=4.56$. The mean *SD* in the Conflict condition was significantly smaller than that in the Path-Integration condition, $t(27)=4.82$, $p<.001$, Cohen's $d=1.29$, but was significantly larger than that in the Landmark condition, $t(27)=2.19$, $p=.04$, Cohen's $d=0.58$. These results indicate variance reduction for the Both condition.

The mean *SD* in the Both condition was consistent with the mean optimal *SD*, $t(27)=0.03$, $p=.97$, Cohen's $d=0.01$, $BF_{01}=6.85$. The mean *SD* in the Conflict condition was significantly larger than the mean optimal *SD*, $t(27)=3.98$, $p<.001$, Cohen's $d=1.06$. The mean observed weight for the landmark (0.88) was significantly larger than the mean optimal weight (0.78), $t(27)=2.42$, $p=.02$, Cohen's $d=0.65$. These results show that the minimum variance was generated for the Both condition but not for the Conflict condition.

Discussion

The evidence of the cue combination for heading estimates in the Both condition (but not in the Conflict condition) obtained in Experiment 3 was congruent with the previous experiments. For goal estimates, the cue combination in the Both condition was achieved for non-home goal estimates (i.e., for the small length ratio 0.5 and the large length ratio 2), even though there was no cue combination for the home with the medium length ratio 1. The cue combination occurred for the small length ratio (i.e., 0.5) but not for the other two medium and large ratios (i.e., 1, 2) in the Conflict condition. These results suggest that the proximal landmarks might have produced estimates for the non-home goals rather than homing, favouring the dual-combination hypothesis over the early-combination hypothesis.

However, the dual-combination hypothesis is not fully supported yet. The dual-combination hypothesis stipulates that both combined self-localisation representations and

proximal landmarks contribute to goal-localisation (Figure 1b). We do not have any evidence indicating that the combined self-localisation representations also affect localising the non-home goals when there are proximal landmarks. One may argue that participants in Experiment 3 might have used path integration and landmarks instead of self-localisation and landmarks in non-home goal-localisation, similar to the suggestion by the late-combination hypothesis.

Experiment 4 was designed to address this concern. The dual-combination hypothesis speculates that a larger length ratio more likely leads to no cue combination, whereas the direct influence of the landmarks leads to cue combination for non-home goal-localisation (Table 1; see elaborated explanation in section "General discussion"). Hence, the disappearance/appearance of cue combination for non-home goal estimates depends on the relative strength of these two opposite effects. The appearance of the cue combination for non-home goal estimates in Experiment 3 might be attributed to a stronger effect from the landmarks than that from the large length ratio. Hence, Experiment 4 used the very large length ratio (length ratio=3) to override the effect from landmarks, which might remove cue combination for goal estimates.

Experiment 4

In Experiment 4, we intended to examine the cue combination in localising a non-home goal if a larger length ratio (PT/TG=3) was adopted for one non-home goal.

Method

Participants. Twenty-eight people (14 men and 14 women, aged 17–21 years) participated in the experiment to fulfil a partial requirement for an introductory psychology course.

Materials, design, and procedure. Experiment 4 was similar to Experiment 3 except for the following changes. Goal B was moved towards the turning point (see Figure 2d) to make the length ratio (PT/TB) increase from two in the prior experiment to three in the present experiment. Specifically, Goal B was located 0.6 m from the turning point (T) in the direction of 330° clockwise relative to the direction of the first leg.

Results

Goal errors. The mean *SDs* of goal errors in the four cue conditions and the mean optimal *SDs* are presented in Figure 8. A two-way repeated-measures ANOVA with cue condition (Path-Integration, Landmark, Both, Conflict) and length ratio of goals (3, 1, 0.5) as independent variables revealed a significant interaction between the cue condition and length ratio of goals, $F(6, 162)=7.94$, $p<.001$, $MSE=157.84$, $\eta_p^2=.23$. Due to the significant interaction,

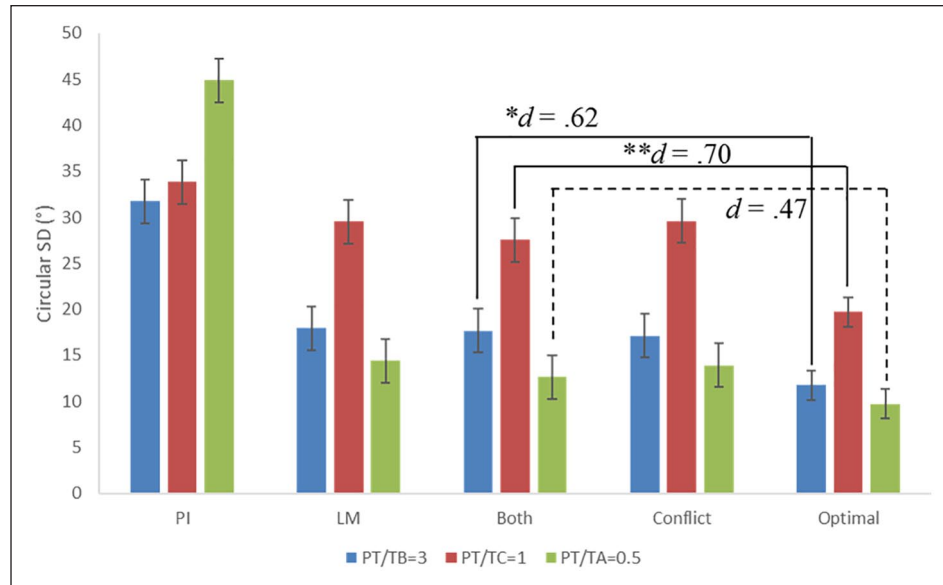


Figure 8. Mean observed SDs of the goal errors (θ) in the Path-Integration (PI), Landmark (LM), Both, and Conflict conditions and the optimal prediction (Optimal) when the length ratio is 3, 1 (home), and 0.5 in Experiment 4. The solid line means a significant difference ($*p < .05$; $**p < .01$) and the dashed line means no significant difference. Error bars represent $\pm SE$ of the mean without removing individual differences.

we analysed the different goals in one-way ANOVAs separately with cue condition as the independent variable.

For Goal B (PT/TB=3) Overall, we found that variance reduction occurred for the Both and Conflict conditions, and minimum variance was achieved for the Conflict condition but not for the Both condition.

In particular, there was a significant main effect of the cue condition, $F(3, 81) = 5.86$, $p = .001$, $MSE = 240.10$, $\eta_p^2 = .18$. The Both and Conflict conditions had significantly smaller mean SDs than the Path-Integration condition, $t(27) = 2.62$, $p = .01$, Cohen's $d = 0.70$ and $t(27) = 2.60$, $p = .02$, Cohen's $d = 0.69$, respectively. The mean SDs in the Both and Conflict conditions were not significantly different from the SD in the Landmark condition, $t(27) = 0.16$, $p = .88$, Cohen's $d = 0.04$, $BF_{01} = 6.77$ and $t(27) = 0.53$, $p = .60$, Cohen's $d = 0.14$, $BF_{01} = 5.99$, respectively. These results indicate that variance reduction occurred for the Both and Conflict conditions.

The Both condition had significantly larger mean SD than the mean optimal SD, $t(27) = 2.32$, $p = .03$, Cohen's $d = 0.62$. The mean SD in the Conflict condition was consistent with the mean optimal SD, $t(27) = 1.95$, $p = .06$, Cohen's $d = 0.52$, $BF_{01} = 1.21$. The mean observed weight for the landmark (0.88) was not significantly different from the mean optimal weight (0.69), $t(27) = 1.83$, $p = .08$, Cohen's $d = 0.49$, $BF_{01} = 1.48$. These results indicate that minimum variance was achieved for the Conflict condition but not for the Both condition.

For Goal C (PT/TC=1, the home) Overall, we found no variance reduction or minimum variance for either two-cue condition.

In particular, the effect of the cue condition did not reach significant, $F(3, 81) = 1.01$, $p = .39$, $MSE = 194.73$, $\eta_p^2 = .04$, indicating no variance reduction for either two-cue condition. The Both and Conflict conditions had significantly larger mean SDs than the mean optimal SD, $t(27) = 2.63$, $p = .01$, Cohen's $d = 0.70$ and $t(27) = 2.58$, $p = .02$, Cohen's $d = 0.69$, respectively. The mean observed weight for the landmark (0.83) was significantly larger than the mean optimal weight (0.56), $t(27) = 3.49$, $p < .01$, Cohen's $d = 0.93$. These results indicate that no minimum variance was achieved for either two-cue condition.

For Goal A (PT/TA=0.5) We found variance reduction and minimum variance for the Both and Conflict conditions.

In particular, there was a significant main effect of the cue condition, $F(3, 81) = 16.82$, $p < .001$, $MSE = 407.14$, $\eta_p^2 = .38$. The Both and Conflict conditions had significantly smaller mean SDs than the Path-Integration condition, $t(27) = 5.20$, $p < .001$, Cohen's $d = 1.39$ and $t(27) = 4.42$, $p < .01$, Cohen's $d = 1.18$, respectively. The mean SDs in the Both and Conflict conditions were not significantly different from the SD in the Landmark condition, $t(27) = .48$, $p = .63$, Cohen's $d = 0.13$, $BF_{01} = 6.12$ and $t(27) = 0.27$, $p = .79$, Cohen's $d = 0.07$, $BF_{01} = 6.61$, respectively. These results indicate that variance reduction occurred for the Both and Conflict conditions.

The mean *SDs* in the Both and Conflict conditions were consistent with the mean optimal *SD*, $t(27)=1.75$, $p=.09$, Cohen's $d=0.47$, $BF_{01}=1.67$ and $t(27)=1.55$, $p=.13$, Cohen's $d=0.41$, $BF_{01}=2.24$, respectively. The mean observed weight for the landmark (0.92) was not significantly different from the mean optimal weight (0.86), $t(27)=0.80$, $p=.43$, Cohen's $d=0.21$, $BF_{01}=5.05$. These results show that the minimum variance was generated for the Both and Conflict conditions.

Heading errors. Overall, we found variance reduction and minimum variance for the Both and Conflict conditions (Figure 5).

In particular, there was a significant main effect of the cue condition, $F(3, 81)=13.72$, $p<.001$, $MSE=286.77$, $\eta_p^2=.34$. The Both and Conflict conditions had significantly smaller mean *SDs* than the Path-Integration condition, $t(27)=4.32$, $p<.01$, Cohen's $d=1.15$ and $t(27)=3.60$, $p=.001$, Cohen's $d=0.96$, respectively. The mean *SDs* in the Both and Conflict conditions were not significantly different from the *SD* in the Landmark condition, $t(27)=.28$, $p=.78$, Cohen's $d=.07$, $BF_{01}=6.60$ and $t(27)=0.81$, $p=.43$, Cohen's $d=0.22$, $BF_{01}=5.00$, respectively. These results indicate that variance reduction occurred for the Both and Conflict conditions.

The mean *SDs* in the Both and Conflict conditions were consistent with the mean optimal *SD*, $t(27)=1.79$, $p=.09$, Cohen's $d=0.48$, $BF_{01}=1.58$ and $t(27)=1.37$, $p=.18$, Cohen's $d=0.37$, $BF_{01}=2.82$, respectively. The mean observed weight for the landmark (0.90) was not significantly different from the mean optimal weight (0.79), $t(27)=1.54$, $p=.14$, Cohen's $d=0.41$, $BF_{01}=2.28$. These results show that the minimum variance was generated for the Both and Conflict conditions.

Discussion

The results of this experiment replicated the cue combination for heading estimates and for the non-home goal with a length ratio of 0.5 but no cue combination for the home with a length ratio of 1 in the Both condition as shown in Experiment 3. Most importantly, no evidence of the cue combination was achieved for the non-home goal with the length ratio being increased to 3 in the Both condition. The results in the Conflict condition were the same as the Both condition except for the cue combination for the non-home goal with the length ratio of 3. These results indicated that combined self-localisation estimates affected localising the non-home goals as well as the home.

General discussion

There are three important findings in the current study. First, when there were distal landmarks, the cue combination appeared in localising goals with a small length ratio

(PT/TG=0.5) but not with a medium (PT/TG=1) or large ratios (PT/TG=2) regardless of localising the home or non-home goals. Second, when there were proximal landmarks, the length ratio affected the appearance of the cue combination in goal estimates differently for the home and non-home goals. In particular, for non-home goals, the cue combination appeared in goal estimates not only for a small length ratio (PT/TG=0.5) but also for a large length ratio (PT/TG=2). The cue combination only disappeared for a very large ratio (PT/TG=3). However, for the home, the cue combination did not occur in home estimates even for a medium length ratio (PT/TG=1). Third, the cue combination occurred in heading estimates regardless of distal or proximal landmarks. The cue combination also occurred in position estimates when proximal landmarks were used to indicate positions (in Experiments 3 and 4, see Supplementary Materials).

To the best of our knowledge, these findings are the first empirical demonstrations of how people combine self-motion cues and landmark cues in goal-oriented navigation beyond homing. Previous studies examined how participants updated their self-localisation relative to goal locations (e.g., Philbeck & Loomis, 1997) and how participants searched for goals using landmarks after disorientation (e.g., Doeller & Burgess, 2008). Previous studies also examined how participants combined self-motion and landmark cues in homing (e.g., Chen et al., 2017). However, there were no studies systematically examining the cue combination of self-motion and landmark cues in goal-oriented navigation other than homing. Consequently, the findings of the current study are important to develop theories of human memory and navigation.

These findings are more consistent with the dual-combination hypothesis than the late-combination hypothesis and early-combination hypothesis (Figure 1). The late-combination hypothesis is an appealing conjecture to conceptualise the relationships between types of spatial memories and methods of navigation (He & McNamara, 2018). According to this conjecture, the process of path integration updates self-to-object vectors whereas the process of piloting updates landmark-to-object vectors. One implication of this conjecture is that these two processes produce two independent estimates. These two estimates are averaged linearly, leading to the minimum estimate variance (cue combination). This hypothesis does not predict any modulation of the length ratio on the cue combination for localising the home or non-home goals. The findings that the cue combination in goal estimates disappeared for large or very large length ratios disapprove of the late-combination hypothesis.

The early-combination hypothesis is an extension of the self-localisation hypothesis for homing (Zhang et al., 2020), assuming that cue interaction in localising non-home goals and homing are the same. According to this speculation, piloting and path integration produce different

estimates of self-localisation representations. Navigators combine these estimates and then pinpoint the combined estimates of self-locations in the mental maps to calculate self-to-object spatial relations. The early-combination hypothesis predicts that the cue combination can occur in self-localisation but not in goal-localisation. When the length ratio is larger, the cue combination in self-localisation is less likely to lead to the appearance of cue combination in goal estimates (Zhang et al., 2020). Importantly, this hypothesis specifies no represented vector between the goals and the proximal landmarks to indicate goal locations regardless of home or non-home goals.

The findings that the length ratio generally modulated the appearance of the cue combination for goal estimates support the early-combination hypothesis over the late-combination hypothesis. However, this hypothesis has difficulty in explaining why the cue combination in goal-localisation appeared more easily for non-home goals than for the home. Especially, in Experiments 3 and 4, while the cue combination disappeared for the home with a length ratio of 1, it disappeared for the non-home goals only when the length ratio increased to 3 but not when the length ratio was 2.

We acknowledge that we did not directly test cue combination for homing using the length ratio of 2 when proximal landmarks were used. We believe that there would be no cue combination for homing for the length ratio of 2 when there were proximal landmarks for the following reasons. First, there was no cue combination for homing for the length ratio of 1 when there were proximal landmarks in the current study (Experiments 3 and 4). Zhang et al. (2020) demonstrated, in theory, simulation, and empirical findings, that when the length ratio increases, it is less likely to observe cue combination for homing. The current study also demonstrated that the larger the length ratio, the less likely to observe cue combination for goal-localisation. Therefore, with the length ratio being increased to 2, there would still be no cue combination for homing. Second, Zhang et al. (2020, Experiments 3 and 4) showed no cue combination for homing when the length ratio of 2 and proximal landmarks were used. Therefore, the finding of cue combination for the non-home goal when the length ratio was 2 should be attributed to the represented vectors between proximal landmarks and non-home goals.

All these findings are consistent with the dual-combination hypothesis. The dual-combination hypothesis is similar to the early-combination hypothesis except that it considers the represented vectors between proximal landmarks and non-home goals. The idea that people can use both self-to-object and inter-object vectors to localise a non-home goal is not new (e.g., Easton & Sholl, 1995). Mou and Spetch (2013) also reported that self-to-object and inter-object vectors were combined to complete goal-localisation. The novelty of this hypothesis is to stipulate that the inter-object vectors only contribute to localising

non-home goals but not to home. This difference occurs because the home and the testing position are strongly connected by the same path (the home as the starting, the testing position as the ending point of the path). However, the locations of the non-home goals are independent of the path and stable in the environment, so are more likely encoded with respect to other salient locations (i.e., landmarks) in the environment. Therefore, people also use landmarks (i.e., inter-object vectors) as the reference points to localising the non-home goals.

Compared with the early-combination hypothesis, the dual-combination hypothesis can readily explain the difference between the homing and localising non-home goals. Nevertheless, we still need to address how the inter-object vectors between the goals and the proximal landmarks could reduce the influence of the length ratio on the appearance of the cue combination in localising non-home goals. In the following section, we will sketch a model based on that developed by Zhang et al. (2020). We will first speculate how the length ratio affects the appearance of the cue combination in goal-localisation without considering the influence of inter-object vectors between the goals and the proximal landmarks (e.g., Experiments 1 and 2). After that, we will speculate how the additional inter-object vectors can reduce the appearance of the cue combination in goal-localisation (e.g., Experiments 3 and 4).

In Figure 9a³ we present schematic relations between the cue combination in heading estimates and goal estimates when distal landmarks specify orientations but not locations (Experiments 1 and 2). The horizontal axis specifies the landmark weight used in heading estimates. As participants' heading estimates are independent of the length ratio PT/TG , there is only one line for the heading error. Because the visual landmarks indicate headings more accurately than self-motion cues do (Zhang et al., 2020), heading errors are larger based on path integration alone (the left end of the landmark weight) than based on landmarks alone (the right end).

There are two lines for the goal error corresponding to the two ratios of PT/TG . When PT/TG is large, the goal error is much smaller in the Path-Integration condition (the left end) than in the Landmark condition (the right end). Its rationale is discussed in Supplementary Materials (see also Zhang et al., 2020). From this figure, we can tell that the variance reduction area, that is, the landmark weights leading to the smallest variance, is closer to the cue that leads to the smaller variance. The reduction area for the heading estimate is closer to the Landmark condition (the right end), whereas the reduction area for the goal estimate is closer to the Path-Integration condition (the left end). Thus, the cue combination in heading estimates to reduce the variance in heading estimates is unlikely to reduce the variance in goal estimates (Zhang et al., 2020). Regarding the line for the small PT/TG , the goal errors for the Path-Integration condition (the left end) and in the Landmark

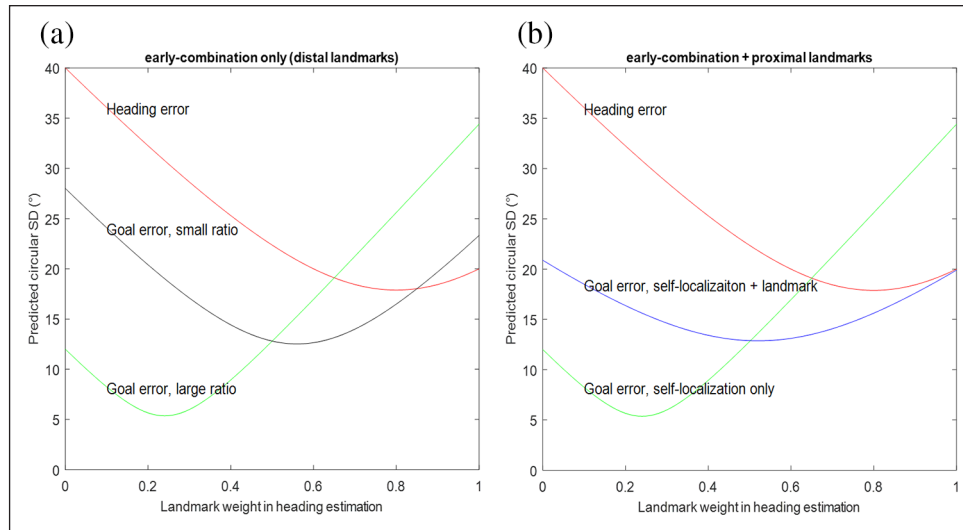


Figure 9. (a) Illustration of the goal estimate based on the early-combination hypothesis only. The green line (light grey) and the black line (dark black) represent the predicted SD of goal errors when the length ratio is large and small, respectively. (b) Illustration of goal estimate, the blue line (dark black) after considering the landmark by equally weighting estimates of the goal locations based on self-localisation representations, the green line (light grey) and based on inter-object vectors, the red line (dark grey), reflecting the heading error.

condition (the right end) are more comparable (see explanations in Supplementary Materials). Therefore, the variance reduction areas for the heading estimate and the goal estimate are close. Consequently, the cue combination in heading estimates to reduce the variance in heading estimates likely also reduces the variance in goal estimates.

In Figure 9b, we consider the direct influence of proximal landmarks in goal-localisation (Experiments 3 and 4). The line of heading error and the line of goal error due to self-localisation with the large ratio are the same as those in Figure 9a (the line of goal error with the small ratio is not plotted). The line of goal error after considering landmarks is added to explain how the inter-object vectors (between proximal landmarks and non-home goals) can reduce distinguishing between cue combinations in heading estimates and goal estimates. We assume that the inter-object vectors between proximal landmarks and the non-home goals are encoded relative to a reference direction in the environment. The errors of using inter-object vectors (especially the direction) between proximal landmarks and the non-home goals to infer the non-home goal location should depend on the errors of identifying the reference direction in the environment. It is reasonable to assume that the errors of the heading estimate reflect the errors of identifying the reference direction in the environment and thus approximate the goal errors based on proximal landmarks (inter-object vectors). As a result, when people combine the estimates of the goal locations based on self-localisation representations (self-to-object vectors) and based on proximal landmarks (inter-object vectors), the variability of the combined estimates should be a result of mixing the lines of goal error due to the self-localisation

and heading error (indicating the errors of using inter-object vectors).

We plot the line of goal estimate (for non-home goals) after considering the landmark by simply equally weighting estimates of the goal locations based on self-to-object vectors (i.e., the line only using self-localisation representations) and based on inter-object vectors (i.e., the line of the heading error). We can see that after considering landmarks, the variance reduction area of the goal error shifts towards the variance reduction area for the heading error. Thus, the cue combination in heading estimates to reduce the variance in heading estimates likely also reduces the variance in goal estimates.

The key difference between the home and non-home goals is that the home location is strongly connected to the participants' testing position by the path whereas goal locations are not strongly connected to the testing position by the path. In addition, the other important difference between them is that goal locations are stable in the environment, whereas the homing location varies in different paths (see Figure 2, Experiments 3 and 4). The current study did not systematically test these two factors. To disentangle these two factors, a future study should factorially manipulate the stability of locations across paths and the goal type. In addition, any non-home goals on the outbound path may also be strongly connected by the path. A future study should investigate whether non-home goals on- or off-path will affect cue combination.

As mentioned in the "Introduction", the format of the cue interaction (cue combination or cue competition) is not relevant to differentiating the three hypotheses that were tested in the current study. However, the data of the current

study are still informative regarding the format of the cue interaction. In the current study, variance reduction for the heading estimates in the two-cue conditions occurred when comparing with the Path-Integration condition but not when comparing with the Landmark condition. Our speculation is that the estimation variability of the two single-cue conditions is quite discrepant. It is more difficult for the two-cue conditions to attain the variance reduction with respect to the more precise single-cue condition (i.e., landmarks). This speculation is slightly different from a landmark dominance cue combination. According to a landmark dominance cue combination, a path integration estimate, even being valid, will be totally ignored (Zhao & Warren, 2015). We tested the landmark dominance cue combination for heading and goal estimates using the observed weights in the conflict condition. The results did not support this possibility (see Supplementary Materials).

In the current study, we only systematically examined the cue combination for the heading error and the goal error but not the position error. In particular, we did not include any real conflict conditions for position estimates in the Conflict condition. We rotated proximal landmarks with respect to the participants' testing position (Chen et al., 2017; Nardini et al., 2008; Zhao & Warren, 2015), which was not able to create two conflicting predictions for the position estimates. As a result, we could not conclusively test the cue combination model in position estimations. Future studies should systematically examine the cue combinations for position estimates.

In conclusion, the current findings support the dual-combination hypothesis in human goal-oriented navigation. To navigate to a remembered goal including the home, people combine self-localisation estimates from piloting and path integration first and then use the combined self-localisation estimates to produce estimates for goal locations including the home. Proximal landmarks produce separate location estimates for non-home goals but not for home. The two location estimates for non-home goals are combined for final estimates but this late combination does not occur for homing, suggesting different mechanisms for homing and goal-oriented navigation.

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Supplementary material

The supplementary material is available at: qjep.sagepub.com.

Notes

1. For example, distal landmarks alone in Experiments 1 and 2 could not indicate positions. Although Experiments 3 and 4 used proximal landmarks, proximal landmarks rotated along with the testing position, and path integration did not produce discrepant position estimates.
2. In Experiments 1 and 2, the rotation of the distal landmarks around the origin (O) and the testing position (P) did not affect participants' estimates of their position and goal locations.
3. To plot the figure (see the simulation method in Zhang et al., 2020), the simulation used the slope of 0.7 and 0.3 for large and small ratios, respectively, in the simulations. The *SD* in estimating heading for Landmark condition and Path-Integration condition were 20 and 40, respectively.

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