# Visual influence on path integration in darkness indicates a multimodal representation of large-scale space

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Our ability to return to the start of a route recently performed in darkness is thought to reflect path integration of motion-related information. Here we provide evidence that motion-related interoceptive representations (proprioceptive, vestibular, and motor efference copy) combine with visual representations to form a single multimodal representation guiding navigation. We used immersive virtual reality to decouple visual input from motion-related interoception by manipulating the rotation or translation gain of the visual projection. First, participants walked an outbound path with both visual and interoceptive input, and returned to the start in darkness, demonstrating the influences of both visual and interoceptive information in a virtual reality environment. Next, participants adapted to visual rotation gains in the virtual environment, and then performed the path integration task entirely in darkness. Our findings were accurately predicted by a quantitative model in which visual and interoceptive inputs combine into a single multimodal representation guiding navigation, and are incompatible with a model of separate visual and interoceptive influences on action (in which path integration in darkness must rely solely on interoceptive representations). Overall, our findings suggest that a combined multimodal representation guides large-scale navigation, consistent with a role for visual imagery or a cognitive map.

How do we find our way in darkness? To answer demands that we identify the internal representations used to guide navigation. Some claim that spatial navigation depends on a coherent multimodal mental model or cognitive map (1–5). Others suggest that such representations do not exist and have been incorrectly inferred from the presence of simpler navigational mechanisms (6–9). One such mechanism is path integration, i.e., the ability to return to the start of a recently walked path by using internal motion-related information, such as proprioceptive and vestibular representations and motor efference copy (referred to hereafter as interoception), which are produced during the outbound path (10–18). Although path integration is primarily thought to depend on interoceptive information, visual information can be used intermittently to prevent the accumulation of error, if available (4, 10, 12, 19).

We asked whether path integration tasks show evidence of a coherent multimodal representation, or whether they reflect separate processes of interoceptive path integration and intermittent use of vision. Our starting point was studies showing that walking on a treadmill in illuminated conditions can affect one's subsequent perception of the translational and rotational speed of walking in darkness (20–23). These studies indicate that control of walking reflects tight coupling between visual and vestibular representations on the one hand and motoric and proprioceptive representations on the other, such that altering the correspondence between these two sets of representations has long-lasting consequences (22, 24). In addition, we know that vision can set the target locations to be reached during navigation performed without vision (19, 25) and that, although such navigation might be guided by interoceptive representations, these

representations are sufficiently abstract to support other actions aimed at the target location, such as throwing (19).

To specifically examine the relationship between visual and interoceptive inputs to navigation, we investigated the effect of manipulating visual information. In the first experiment, we investigated whether visual information present during the outbound trajectory makes an important contribution to the generation of the return path in addition to interoception. In the second experiment, we investigated whether motion-related interoceptive inputs and exteroceptive visual inputs contribute separately to determining the return path, or whether both types of information are combined to form a single multimodal representation first. The former separate-inputs model is consistent with the classical model of path integration in a wide variety of animals, in which interoceptive information is integrated to indicate movement direction, and visual information is used to correct cumulative error, provide orientation, or an alternative direction via piloting (11, 26–29). The latter multimodal representation model is consistent with the use of a single mental model or cognitive map of the environment abstracted from both types of information, as has been argued for mammalian spatial navigation by some (1, 2, 5), but not others (6–9). It would also be consistent with the suggestion that the perceptuo-motor control of walking includes an abstract cognitive component (19, 22, 24, 25). In Discussion, we compare our findings to the two models and propose a quantitative framework for predicting the effects of visual manipulations within the multimodal model.

## Results

**Experiment 1: Effect of Visual Gain During an Illuminated Outbound Path on Returning in Darkness.** A guided outbound path was performed in an immersive virtual reality (VR) environment to allow decoupling of visual input from participants' actual motion (Fig. 1A). A navigated return path was then performed in darkness.

Separate groups performed the outbound path under manipulations of either rotational or translational gain. All participants experienced four conditions: a visual projection with 1.3×, 1×, and 0.7× the gain of the actual movement, and following the outbound path in darkness. We checked that participants did not adapt to any of the gain conditions (i.e., show long-term effects that might affect responses in subsequent conditions) by taking a reference measure before and after the gain conditions was compared. For rotational gains, the angle walked before and after the main experiment did not change [$t(15) = 0.60$, $P = 0.56$].
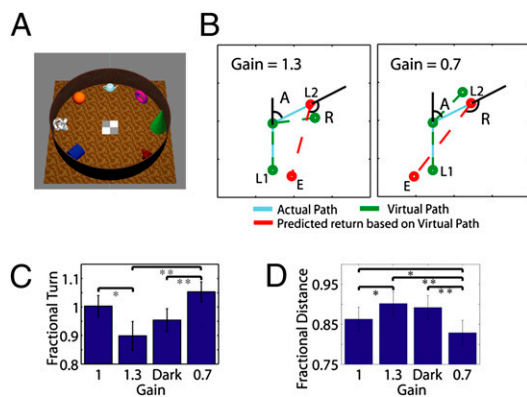
**Fig. 1.** Effects of visual gain manipulations during the outbound path on the return path taken in darkness (experiment 1). (*A*) The virtual room consisted of seven large objects in the periphery of a circular room of diameter 14 m, with a parquet floor, 2-m-high brick wall, and gray and white tiles indicating the center. (*B*) Predictions for participants' return paths in darkness based on their visual perception of the outbound path (virtual path, cf. actual path) under a visual rotation manipulation. L1 and L2 show the start and end of the leading phase, respectively. E shows the end of the return path if visual information dominates. For example, participants should overturn under visual rotation gain of 0.7 (*Right*) due to underestimation of the outbound turn angle A, and their return angle R will be increased. (*C*) The FT (actual return angle R/veridical angle) for different rotation gain conditions. (*D*) The FD (actual return distance/veridical distance) for different translation gain conditions. Error bars show SE. Horizontal lines indicate significant pairwise comparisons, *$P < 0.05$; **$P < 0.01$.

For translational gains, the distance walked before and after the main experiment did not change [$t(15) = -0.73$, $P = 0.48$].

The main measure of participants' responses was either the fractional turn (FT) made (i.e., actual/veridical turn angle) or the fractional distance (FD) walked (i.e., actual/veridical distance) on the return path. Veridical turn or distance refers to the physical path walked and so corresponds to accurate interoceptive representations and to accurate visual representations when the visual gain is 1. Fig. 1*B* illustrates how under/overestimate of the angle turned during the outbound path affects the FT made for the return path for rotation gains. Consider the left schematic in Fig. 1*B*: a visual rotation gain of 1.3 relative to the physical turn. Blue lines indicate the physical path the participant is led through (two legs, L1 and L2, separated by turn A). Green lines indicate the virtual path shown by the visual projection. If participants ignore all visual information they should return accurately to the start (L1). If participants rely entirely on the visual information, they will make a return angle (R) indicated by the red line, i.e., they will underturn and miss the start (L1), giving an FT <1.

The SD for FTs and FDs was 0.36 and 0.20, respectively, and did not vary with the size of the gain [one-way ANOVA on the variance of FTs and FDs showed no main effect of gain: $F(3, 45) = 0.165$, $P = 0.92$ and $F(3, 45) = 0.56$, $P = 0.65$, respectively]. For both rotation and translation gains, mixed ANOVAs were performed with factors, path, visual gain, and gender. The direction of the outbound turn was an additional factor for the rotation manipulation. No main effects of turn direction or gender were found. Fig. 1 *C* and *D* show the significant main effect of gain on participants' responses for both manipulations [for rotation, $F(3, 42) = 5.00$, $P = 0.005$; for translation, $F(3, 42) = 7.96$, $P < 0.001$]. For both the rotation and translation manipulations, responses made when the gain was 1.3 were significantly different from when the gain was 0.7 and in the predicted direction (Fig. 1; pairwise comparisons between rotation gains 1 and 1.3: $P = 0.036$; between 1.3 and 0.7: $P = 0.008$; between dark and 0.7: $P = 0.002$; pairwise comparisons between translation gains 1 and 1.3: $P = 0.025$; between 1 and 0.7: $P = 0.019$; between 1.3 and 0.7: $P < 0.001$; be-

tween dark and 0.7: $P = 0.004$). This suggests that visual inputs strongly influence returning in darkness to the start of an outbound path traversed in lit conditions.

The fractional distance measure was always less than 1, reflecting a general underestimation of visual distances occurring in VR (30–34). A main effect of the shape of the outbound path was also found (Fig. S1) and is discussed in *SI Materials and Methods*.

Postexperiment participant debriefs suggest the use of visual imagery in the path integration task. When questioned on whether participants used a particular strategy, 26 of 32 answered that they imagined their trajectory either within the virtual room or as straight line paths, or imagined a bird's eye view to consider their location.

**Experiment 2: Effect of Adaptation to Visual Gain on Triangle Completion in Darkness.** In experiment 1, we verified that visual experience during the outward path influences the return path made in darkness. In experiment 2, participants performed a triangle completion task (returning to the start of a two-legged outbound path) entirely in the dark, ruling out any direct role of visual input. Instead, participants were trained with modified visual feedback (rotation gain of 0.7) over an extended period to enable us to examine the subsequent effects of this experience on the performance of triangle completion in darkness. We believe these findings indicate that path integration is guided by a mental model that combines both visual and interoceptive inputs, and that may be related to visual imagery (*Discussion*).

Fig. 2 *A* and *B* show the change in two reference measures taken before and after exposure to a 0.7 rotation gain. Repeated-measures ANOVA showed significant changes in the angle rotated after the adaptation phase, in the expected direction, for both the instructed turns and sound localization turns [$F(1, 19) =$
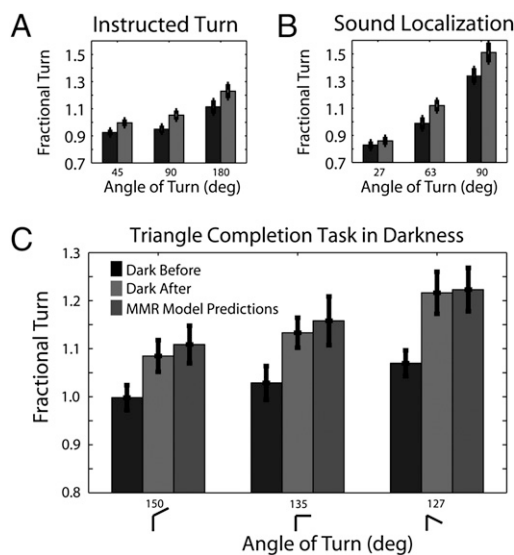


**Fig. 2.** The effect of adaptation to a visual rotation gain of 0.7 (experiment 2). (*A*) FT (actual return angle/veridical angle) values when participants are instructed to rotate through one of three angles, before and after the adaptation phase. (*B*) FT values when participants rotated to face a sound at one of three locations, before and after the adaptation phase. (*C*) FT values when performing triangle completion entirely in darkness before and after the adaptation phase, shown individually for the three outbound paths. Also shown are the predictions of the MMR model (Fig. 3) using the reference turns in Fig. 2*A* to estimate the extent of each participant's adaptation (*Discussion*). Numbers on the x axes indicate the correct return angles for the outbound paths taken. Dark Before and Dark After correspond to phases 1 and 4 of experiment 2 for *A* and *B*, and phases 2 and 5 for *C* (*Materials and Methods*).

25.27, $P < 0.001$ and $F(1, 19) = 14.60$, $P = 0.001$, respectively]. This indicates that participants showed long-term adaptation to the visual gain applied during the adaptation phase.

Comparing the triangle completion phases of the experiment before and after adaptation, the FTs show a significant influence of visual adaptation on the return directions chosen (Fig. 2C). The SD of all participants' FTs was 0.16. A repeated-measures ANOVA on the variance of individual participants' return angle showed no main effects for phase or path, suggesting that the consistency of individuals' responses were not affected by adaptation [$F(1, 19) = 1.48$, $P = 0.24$ and $F(2, 38) = 1.71$, $P = 0.20$, respectively]. Repeated-measures ANOVA on FT in the triangle completion task showed a main effect of adaptation [$F(1, 19) = 16.12$, $P = 0.001$]. There was also a main effect of path [$F(2, 38) = 13.12$, $P < 0.001$], but no interaction such that the mean FT on each path showed the adaptation effect in the appropriate phase.

## Discussion

Having shown that path integration is affected by visual as well as interoceptive information in experiment 1, we adapted subjects to a 0.7 rotation gain in experiment 2. The canonical paradigm for investigating path integration is triangle completion, in which the participant must use internal representations of a two-legged outward path to determine the return leg. The nature of these representations is unknown. At minimum, the vector to the start must be maintained; at maximum, a complete representation of the path traversed so far and surrounding environment might be maintained.

We contrast two schematic models of the functional organization of behavior during triangle completion (Fig. 3). Both models contain three types of representation: visual, interoceptive, and motoric. Motor output is controlled via the feedback loops conveying the visual and interoceptive consequences of action. In the separate inputs (SI) model these feedback loops remain separate, whereas in the multimodal representation (MMR) model they are combined into a single MMR. We assume that the mapping from motor representations to interoceptive representations (comprising motor efference copy and the proprioceptive and vestibular consequences of motion, none of which we manipulate) remains 1:1 throughout the experiment. By contrast, modifying the rotation or translation gain of the visual projection in immersive VR causes a mismatch between visual representations on one hand and motoric and interoceptive representations on the other.

In experiment 1 we varied the rotation and translation gain of the visual VR environment during the outbound trajectory and

measured the return trajectory made in darkness. The results indicate a highly significant influence of the visual information available at the end of the outbound path upon the choice of return direction, even though the return path was performed in darkness, and therefore presumably under the control of interoceptive feedback. This strong influence of vision may reflect the relative reliability associated with this type of input in the rich, fully lit virtual environment traversed by the outbound path (35). However, although experiment 1 confirms a role for visual input in path integration tasks, it does not distinguish between the two models in Fig. 3. Nevertheless, participant debriefs report of imagining the outbound path suggest a single explicit internal representation.

In experiment 2, participants were trained in the immersive virtual environment with modified visual gain, so as to examine any subsequent effects on triangle completion performed entirely in the dark. In this situation, the two models in Fig. 3 make different predictions.

**Separate Inputs Model.** While training to reach visual targets under modified visual gain, action is likely to be controlled via visual feedback of location and orientation relative to the target. In this case the gain of the mapping between visual and motoric representations is not important (action simply has to reduce the difference between actual location/orientation and target) and probably would not show long-term adaptation. However, even if the visual to motor mapping showed adaptation, it would not affect triangle completion performed in darkness because there is no visual input, and action is controlled solely by interoceptive representations. Our finding of a significant effect of adaptation on navigation in darkness (Fig. 2) clearly rules this out.

We assume that the mapping between interoceptive and motor representations remains 1:1, because our manipulation affects neither type of representation. Even so, it is worth noting that a simple recalibration of this mapping would not predict our result, because this would imply similar change in the FT measure across the three outbound paths. A repeated-measures ANOVA on the FT ratio for all conditions, including controls, with factors path and trial type, showed a significant effect of path, in which FT increased with increasing turn angle in the path [$F(2, 38) = 4.17$, $P = 0.023$]. Alternatives to the SI model, in which visual adaptation affects interoception, or in which interoception can drive visual representations in darkness, require connections between visual and interoceptive representations, effectively creating a version of the MMR model, which we consider next.

**Multimodal Representation Model.** Both visual and interoceptive representations contribute to a MMR, with a significant influence of vision during navigation in the virtual environment. This strong visual influence on the MMR is seen in experiment 1, where the visual gain manipulation alters the return direction chosen at the end of the outbound path, consistent with the visual perception of turns made during the outbound path. During the training to reach visual targets under modified visual gain experienced in experiment 2, action is controlled by visual and/or interoceptive feedback via the MMR, with visual input likely to dominate. The strong visual influence on the MMR means that the visual gain manipulation will introduce a mismatch between the MMR and interoceptive representations. Thus prolonged exposure to modified visual gain will change the gain of the mapping from interoceptive representations to the MMR. [This model can be seen as one way of implementing the perceptuo-motor coupling suggested for control of walking (22, 24) in the context of path integration.] During navigation in darkness, the MMR is driven solely by interoceptive representations, and the MMR controls motor output. In this model, unlike the SI model, an effect of adaptation is predicted because of the altered mapping from interoceptive representations to the MMR. After adaptation to visual gain 0.7, this alteration causes the interoceptive input during the outbound path
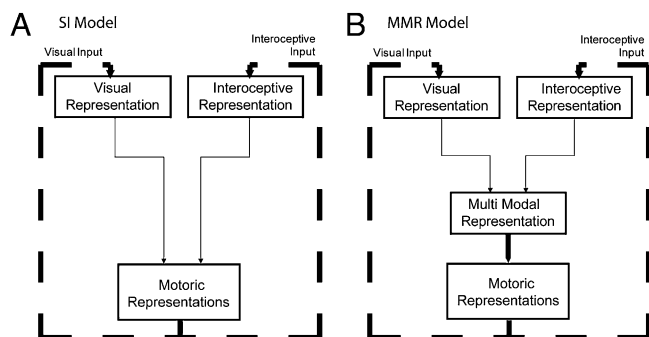


**Fig. 3.** Schematics of two possible models controlling movement. Both include separate visual and interoceptive (proprioceptive, vestibular, and motor efference) inputs. Full lines indicate connections between representations; dashed lines indicate the visual and interoceptive consequences of action. (A) SI model shows action as a result of separate visual and interoceptive inputs, e.g., interoceptive path integration occasionally reset by visual input. (B) MMR model shows visual and interoceptive inputs combined into a coherent MMR that controls action.

to produce a MMR which underestimates the outbound turn. The consequence of this is an increased FT in the return direction after adaptation compared with before adaptation (Fig. 1B, gain = 0.7). Fig. 2C illustrates our findings.

This model can be used to make quantitative predictions. Suppose that training with visual gain $G_v$ causes partial recalibration of the interoceptive input to the MMR equivalent to a gain $G_i$. For experiment 2, $G_v = 0.7 < G_i < 1$. If the outbound path comprises two equal legs joined by a turn angle $A$, the correct return angle is $180 - A/2$ (Fig. 1B). However, the outbound turn angle in the MMR driven by the altered mapping from interoceptive input will be $A' = G_i A$, indicating a return angle $R' = 180 - G_i A/2$ in the MMR. In addition, if production of the return angle is controlled by the MMR driven by the altered mapping from interoceptive input, the actual angle turned through will be $R = R'/G_i$. This will produce an adaptation-dependent FT (actual angle turned/correct return angle) of

$$FT = R/(180 - A/2) = (R'/G_i)/(180 - A/2)$$
$$= (180/G_i - A/2)/(180 - A/2) \qquad [1]$$

Finally, each participant's natural propensity to overturn (in the absence of adaptation) is taken into account by multiplying the above adaptation-dependent FT predicted by the MMR model by each participant's FT on each path before adaptation (Fig. 2C, Dark Before).

We can estimate the gain induced in the interoceptive to MMR mapping ($G_i$) from the ratio of the reference turns made before and after adaptation training (turn angle after/turn angle before; Fig. 2A). The value of $G_i$ appropriate to a given outbound turn angle $A$ is found by interpolation between the reference angles performed (45°, 90°, 180°). The pattern of predicted FTs closely matches the observed values (Fig. 2C, MMR model predictions). The model can be further assessed by regression of the predicted FTs against the actual FTs (across participants) for the paths used in experiment 2, after adaptation (Fig. 4).

We also performed the adaptation experiment with a rotation gain of 1.3. However, unlike for the 0.7 gain in experiment 2, there was no significant evidence of adaptation in the reference turn measures (instructed turn and sound localization turn; Fig. S2 A and B). It may be that the increased visual motion with a gain of 1.3 was enough to override participants' prior assumption that the world is static, thus preventing proper immersion in the VR environment. Some evidence toward this comes from participant debriefs; 6 of 20 participants in this experiment reported feeling dizzy during the 1.3 rotation gain experiment, compared with none when the rotation gain was 0.7. Notwithstanding the absence of a consistent effect of adaptation, participants' Reference Turn values can still be used with the MMR model (Eq. 1) to accurately
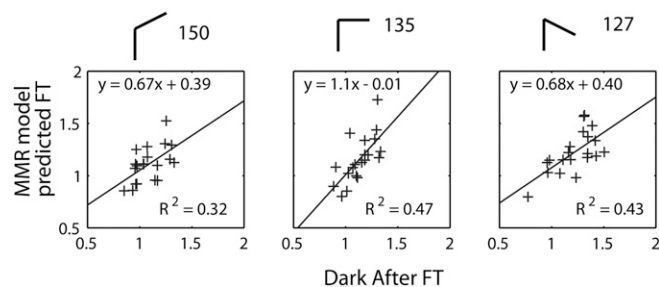
predict their FTs in triangle completion in this experiment (Figs. S2C and S3).

Although we did not deliberately manipulate the reliability of visual and interoceptive information, we would expect that their relative contributions to the multimodal representation to reflect Bayesian weighting by signal noise. This appears to be a common feature of multimodal integration in decision making (36–38), magnitude estimation (39–41), and in combining conflicting visual and interoceptive cues to location (35).

Accurate spatial navigation to a location that is not simply indicated by a direct perceptual cue or a well-learned route appears to depend on the hippocampal formation in mammals (2–4, 42, 43). Neurons in the hippocampal formation provide a multimodal representation of location and orientation, via the firing of place cells, grid cells, and head direction cells (2, 44–48). Thus, the hippocampal formation may support the multimodal representation of spatial location implicated by our studies and by other experiments indicating the presence of cue-cue associations in navigation [associations between interoceptive and visual representations in this case (9)]. These representations likely drive egocentric imagery in parietal areas (49), another area associated with path integration (50) and multimodal representations of location (51). A close link between visual imagery and spatial navigation is supported by the observed correlation between symptoms of imaginal (but not perceptual) neglect and navigation in neuropsychological patients with unilateral damage (52), and by deficits in imagery following hippocampal damage (53).

Finally, we note that MMR and SI processes probably both exist, and operate in parallel. Thus, although the MMR model strongly influences behavior in the current experiment, different experimental conditions, or loss or dysfunction of the MMR, could cause greater reliance on direct connections from interoception to motor output: reducing the effect of visual adaptation. The presence of multiple parallel mechanisms capable of supporting triangle completion in different ways would be consistent with a multiple-systems view of memory in which the striatum supports the more direct interoceptive-motoric representation of routes (42, 43). The presence of multiple parallel systems might also explain conflicting reports of the effects of hippocampal lesions on path integration tasks, in which some studies report deficits (54, 55) and others do not (56–58). We would predict an intact ability to perform triangle completion, but no effect of visual adaptation, in mammals with hippocampal lesions.

To conclude, in experiment 1, we showed that visual and interoceptive information from the outbound path contributes to returning to the starting position in darkness. This is consistent with many studies, showing that visual cues play a role in such tasks, not least in correcting the accumulation of error inherent in interoceptive path integration (27, 35, 59, 60). Subjective reports in this experiment suggested that visual imagery plays a role in calculating the return direction.

In experiment 2 we went a step further in showing that visual and interoceptive information are combined into a single multimodal representation that is used to guide navigation. This model makes quantitative predictions matching the observed effect of prior adaptation to manipulations of visual gain on triangle completion performed entirely in darkness. The model is consistent with the perceptuo-motor coupling previously seen in the control of walking (22, 24). The alternative model, of separate visual and interoceptive inputs to the motor system, predicts no such effects.

Overall, our findings support a role for a multimodal representation or cognitive map (2) in guiding navigation, even in the archetypal example of interoceptive path integration: triangle completion in darkness.



**Fig. 4.** Regression of MMR model predicted FTs against actual FTs in experiment 2 after adaptation to visual gain (Fig. 2C). Each point represents one participant. The outbound paths are indicated above each graph as well as the correct return angle (degrees).

## Materials and Methods

Subjects performed path integration in an immersive VR environment. Here they were able to freely move around while wearing 3D goggles that projected

the visual world to their eyes. The visual world was programmed using Virtools 3.5. Tracking was performed using the VICON IQ 2.5 tracking system. Participants carried out the experiment in a room with dimensions 7.55 × 6.15 m. Participants wore an eMagin z800 head-mounted display (horizontal × vertical resolution = 800 × 600), with field of view of 40° diagonally (32 × 24°), a 100% overlap, and a refresh rate of 30 Hz.

For both experiments, bricks ranging in width between 15 and 40 cm × 11-cm high formed a circular VR room 14 m in diameter and 3 m high. Parquet flooring with wooden blocks of the size 75 × 18.75 cm covered the floor. At seven peripheral locations were objects that assisted the participant's self-orientation. Starting from the top and going clockwise were a light blue teapot, a purple ring, a green cone, a monkey, a blue cylinder, a torus knot, and an orange. A checkerboard pattern marked the middle of the room (Fig. 1A).

Postexperiment, participants answered a list of open questions (*SI Materials and Methods*) designed to probe task performance strategies and confirm that the external room had no direct influence on their responses.

**Procedure in Experiment 1: Influence of Visual Input on Path Integration** Sixteen participants each were recruited for the translation and rotation experiment, balanced across gender with an age range of 19–32. Participants did not see the actual room before or during the experiment. Participants wore earplugs to mask out background noise in the room. Participants were also not shown the actual room before or during the experiment.
*Reference measure.* At the beginning and end of the experiment a football (reference object) was placed in the VR room, 15° to the observer's left for a period of 5 s. After this the screen became black and observers walked to the ball. This was used as a measure of how accurately they walked to a previously viewed target. This would then be compared with a reference measure after the main experiment to check whether there were any adaptation effects during the experiment.
*Test trials.* In both the translation and rotation experiment, participants were led along nine different paths (shown in Fig. S1A). All participants experienced the same four paths as practice at the beginning, after which path sequence proceeded in a pseudorandom order. Participants always started the path in the same position in the VR room, at 6 o'clock 4 m away from the center of the room facing north in the direction of the teapot. This ensured that all participants experienced roughly the same optic flow patterns and were not biased across trials as a result of relative landmark differences. Participants viewed the room while being led along the path. At this point, the room would be replaced by a dark screen, whereby participants would have to return to where they thought their origin was. Participants were then led to a new start position in the real room, to ensure that distances to the physical start position could not be used to error correct their previous response. Participants then proceeded with the next trial.

The gain in the virtual room was 1 for the first four practice trials. After this the gain in the room varied in the following order: 1, 1.3, dark, 0.7. This order was to ensure that participants did not adapt to a particular gain value across trials. Participants carried out 36 trials after practice.

**Procedure in Experiment 2: Influences of Prior Visual Adaptation on Triangle Completion in Darkness.** Twenty participants were recruited: 11 females and 9 males with an age range of 19–35 for gain = 0.7. With the exception of the phase where the reference measures were taken, participants wore earplugs to mask out background noise in the room. Participants were also not shown the physical room before or during the experiment. The experiment consisted of five distinct phases.
*(i) Reference measures.* Participants viewed the VR room and were instructed to face the teapot. A sound announced when participant's viewing direction

was less than ±5° for 2 s. The experimenter then initiated either of two reference tasks in a pseudorandom order.

In the sound localization reference task, the experimenter would stand at one of three positions relative to the participant [(1, 2) (2, 1), or (2, 0) m] and play the sound of an old bicycle horn (found to be most localizable in a pilot study) in three sharp bursts. Participants then rotated toward the direction of the sound. Because of the difficulty in locating a novel sound in an unfamiliar environment, participants practiced localizing the sound at the three locations at least twice before the experiment began. A cloth covering their head obscured any visual information.

In the instructed turn task, on-screen instructions asked participants to rotate by 45°, 90°, or 180°.

Following their response, participants rotated back, causing the VR room to reappear. Each rotation and sound localization was repeated three times.
*(ii) Dark before.* Participants performed triangle completion in the dark. They were led on one of three L-shaped paths, following which they turned and walked the shortest distance back to their start alone. A wooden pole of length 43 cm and diameter 2.5 cm held between participant and experimenter allowed the experimenter to precisely control the participant's turns of 63°, 90°, or 117°, which separated the two 2-m legs of the path. Participants were informed that they started at different places between trials and were therefore unable to use information about their return to assess their error on the last trial.
*(iii) Visual adaptation.* Participants then performed a subsidiary task in the VR room, which had an associated rotation gain. Participants were not made aware of the gain in the environment and did not notice it. The task consisted of a football appearing at the participant's head height. Participants walked to the ball until it disappeared. At this point, participants were instructed to keep their feet still but were allowed to rotate their head or body to view the room. Participants then indicated which quadrant of the room they were in: top left, top right, bottom left, or bottom right. The football then reappeared in another location in the room, requiring participants to repeat the self-location process. At least 25 trials were performed.
*(iv) Reference measures.* Participants repeated phase (i).
*(v) Dark after.* Three control conditions were randomly interleaved with the original L-shaped triangle completion task. Two were distraction tasks, where on-screen text 30 pixels high and 320 pixels wide accompanied triangle completion. Participants practiced each distraction trial before the main experiment. During distraction (digits) controls, participants saccaded to and verbally reported a randomly generated number between 0 and 99 that appeared at a random position on the screen at a frequency of 1 Hz. In distraction (words) controls, words appeared at the same place in the middle of the screen, also at 1 Hz, which participants read while performing triangle completion.

During temporal delay controls, a 10-s delay separated the leading and response stage requiring participants to wait before they returned to the start. Assessment of these controls can be found in *SI Materials and Methods* and Fig. S4.

1. Tolman EC (1948) Cognitive maps in rats and men. *Psychol Rev* 55:189–208.
2. O'Keefe J, Nadel L (1978) *The Hippocampus as a Cognitive Map* (Oxford Univ Press, New York).
3. Morris RGM, Garrud P, Rawlins JN, O'Keefe J (1982) Place navigation impaired in rats with hippocampal lesions. *Nature* 297:681–683.
4. Burgess N, Maguire EA, O'Keefe J (2002) The human hippocampus and spatial and episodic memory. *Neuron* 35:625–641.
5. Wolbers T, Hegarty M (2010) What determines our navigational abilities? *Trends Cogn Sci* 14:138–146.
6. Wang RF, Spelke ES (2002) Human spatial representation: Insights from animals. *Trends Cogn Sci* 6:376–382.
7. Bennett ATD (1996) Do animals have cognitive maps? *J Exp Biol* 199:219–224.
8. Mackintosh NJ (2002) Do not ask whether they have a cognitive map, but how they find their way about. *Psicologia* 23:165–185.
9. Pearce JM (2009) The 36th Sir Frederick Bartlett lecture: An associative analysis of spatial learning. *Q J Exp Psychol (Colchester)* 62:1665–1684.
10. Mittelstaedt H, Mittelstaedt ML (1973) Mechanismen der Orientierung ohne richtende Aussenreize. *Fortschr Zool* 21:45–58.
11. Mittelstaedt H (2000) Triple-loop model of path control by head direction and place cells. *Biol Cybern* 83:261–270.
12. Wehner R, Srinivasan MV (1981) Searching behavior of desert ants, genus Cataglyphis (Formicidae, Hymenoptera). *J Comp Physiol* 142:315–338.
13. Gallistel CR (1990) *The Organization of Learning* (MIT Press, Cambridge, MA).
14. Loomis JM, et al. (1993) Nonvisual navigation by blind and sighted: Assessment of path integration ability. *J Exp Psychol Gen* 122:73–91.
15. Harris LR, Jenkin M, Zikovitz DC (2000) Visual and non-visual cues in the perception of linear self-motion. *Exp Brain Res* 135:12–21.
16. Telford L, Howard IP, Ohmi M (1995) Heading judgments during active and passive self-motion. *Exp Brain Res* 104:502–510.
17. Chance SS, et al. (1998) Locomotion mode affects the updating of objects encountered during travel: The contribution of vestibular and proprioceptive inputs to path integration. *Presence* 7:168–178.

18. Kearns MJ, Warren WH, Duchon AP, Tarr MJ (2002) Path integration from optic flow and body senses in a homing task. *Perception* 31:349–374.

19. Thomson JA (1980) How do we use visual information to control locomotion? *Trends Neurosci* 3:247–250.

20. Durgin FH, et al. (2005) Self-motion perception during locomotor recalibration: More than meets the eye. *J Exp Psychol Hum Percept Perform* 31:398–419.

21. Mohler BJ, et al. (2007) Calibration of locomotion resulting from visual motion in a treadmill-based virtual environment. *ACM Trans Appl Percept*, 10.1145/1227134.1227138.

22. Pick HL, et al. (1999) The recalibration of rotational locomotion. *J Exp Psychol Hum Percept Perform* 25:1179–1188.

23. Rieser JJ, Pick HL, Jr., Ashmead DH, Garing AE (1995) Calibration of human locomotion and models of perceptual-motor organization. *J Exp Psychol Hum Percept Perform* 21:480–497.

24. Rieser JJ, Pick HL (2007) Using locomotion to update spatial orientation. *The Emerging Spatial Mind*, eds Plumert J, Spencer JP (Oxford Univ Press, New York), pp 77–103.

25. Loomis JM, et al. (1996) Visual perception of location and distance. *Curr Dir Psychol Sci* 5:72–77.

26. Etienne AS, Maurer R, Boulens V, Levy A, Rowe T (2004) Resetting the path integrator: a basic condition for route-based navigation. *J Exp Biol* 207:1491–1508.

27. Collett M, Collett TS (2000) How do insects use path integration for their navigation? *Biol Cybern* 83:245–259.

28. Etienne AS, Maurer R, Séguinot V (1996) Path integration in mammals and its interaction with visual landmarks. *J Exp Biol* 199:201–209.

29. Foo P, Warren WH, Duchon A, Tarr MJ (2005) Do humans integrate routes into a cognitive map? Map- versus landmark-based navigation of novel shortcuts. *J Exp Psychol Learn Mem Cogn* 31:195–215.

30. Creem-Regehr SH, Willemsen P, Gooch AA, Thompson WB (2005) The influence of restricted viewing conditions on egocentric distance perception: Implications for real and virtual indoor environments. *Perception* 34:191–204.

31. Richardson AR, Waller D (2007) Interaction with an immersive virtual environment corrects users' distance estimates. *Hum Factors* 49:507–517.

32. Thompson WB, et al. (2004) Does the quality of the computer graphics matter when judging distances in visually immersive environments? *Presence* 13:560–571.

33. Wann JP, Rushton S, Mon-Williams M (1995) Natural problems for stereoscopic depth perception in virtual environments. *Vision Res* 35:2731–2736.

34. Witmer BG, Kline PB (1998) Judging perceived and traversed distance in virtual environments. *Presence* 7:144–167.

35. Nardini M, Jones P, Bedford R, Braddick O (2008) Development of cue integration in human navigation. *Curr Biol* 18:689–693.

36. Cheng K, Shettleworth SJ, Huttenlocher J, Rieser JJ (2007) Bayesian integration of spatial information. *Psychol Bull* 133:625–637.

37. Körding K (2007) Decision theory: What "should" the nervous system do? *Science* 318:606–610.

38. Glennerster A, Tcheang L, Gilson SJ, Fitzgibbon AW, Parker AJ (2006) Humans ignore motion and stereo cues in favor of a fictional stable world. *Curr Biol* 16:428–432.

39. Lourenco SF, Longo MR (2010) General magnitude representation in human infants. *Psychol Sci* 21:873–881.

40. Cheng K, Spetch ML, Miceli P (1996) Averaging temporal duration and spatial position. *J Exp Psychol Anim Behav Process* 22:175–182.

41. Walsh V (2003) A theory of magnitude: Common cortical metrics of time, space and quantity. *Trends Cogn Sci* 7:483–488.

42. White NM, McDonald RJ (2002) Multiple parallel memory systems in the brain of the rat. *Neurobiol Learn Mem* 77:125–184.

43. Hartley T, Maguire EA, Spiers HJ, Burgess N (2003) The well-worn route and the path less traveled: Distinct neural bases of route following and wayfinding in humans. *Neuron* 37:877–888.

44. Muller R (1996) A quarter of a century of place cells. *Neuron* 17:813–822.

45. Hafting T, Fyhn M, Molden S, Moser MB, Moser EI (2005) Microstructure of a spatial map in the entorhinal cortex. *Nature* 436:801–806.

46. Taube JS (1991) Space, the final hippocampal frontier? *Hippocampus* 1:247–249.

47. Ekstrom AD, et al. (2003) Cellular networks underlying human spatial navigation. *Nature* 425:184–188.

48. Doeller CF, Barry C, Burgess N (2010) Evidence for grid cells in a human memory network. *Nature* 463:657–661.

49. Byrne P, Becker S, Burgess N (2007) Remembering the past and imagining the future: a neural model of spatial memory and imagery. *Psychol Rev* 114:340–375.

50. Save E, Guazzelli A, Poucet B (2001) Dissociation of the effects of bilateral lesions of the dorsal hippocampus and parietal cortex on path integration in the rat. *Behav Neurosci* 115:1212–1223.

51. Andersen RA, Snyder LH, Bradley DC, Xing J (1997) Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annu Rev Neurosci* 20:303–330.

52. Guariglia C, Piccardi L, Iaria G, Nico D, Pizzamiglio L (2005) Representational neglect and navigation in real space. *Neuropsychologia* 43:1138–1143.

53. Hassabis D, Kumaran D, Vann SD, Maguire EA (2007) Patients with hippocampal amnesia cannot imagine new experiences. *Proc Natl Acad Sci USA* 104:1726–1731.

54. Maaswinkel H, Jarrard LE, Whishaw IQ (1999) Hippocampectomized rats are impaired in homing by path integration. *Hippocampus* 9:553–561.

55. Worsley CL, et al. (2001) Path integration following temporal lobectomy in humans. *Neuropsychologia* 39:452–464.

56. Alyan S, McNaughton BL (1999) Hippocampectomized rats are capable of homing by path integration. *Behav Neurosci* 113:19–31.

57. Shrager Y, Kirwan CB, Squire LR (2008) Neural basis of the cognitive map: Path integration does not require hippocampus or entorhinal cortex. *Proc Natl Acad Sci USA* 105:12034–12038.

58. Wiener JM, Berthoz A, Wolbers T (2010) Dissociable cognitive mechanisms underlying human path integration. *Exp Brain Res*, 10.1007/s00221-010-2460-7.

59. Séguinot V, Maurer R, Etienne AS (1993) Dead reckoning in a small mammal: The evaluation of distance. *J Comp Physiol A* 173:103–113.

60. Sommer S, von Beeren C, Wehner R (2008) Multiroute memories in desert ants. *Proc Natl Acad Sci USA* 105:317–322.

NEUROSCIENCE

# Supporting Information

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### SI Materials and Methods

**Main Effect of Path for Experiment 1.** When analyzing the FT and FD walked in experiment 1, the same mixed ANOVA that showed a main effect of different gain conditions (but no main effects of gender or turn direction) also showed a main effect of path for the two gain manipulations (see Fig. S1*A* for the paths used in the rotation and translation gain manipulations of experiment 1). For the rotation gains, the path used had an overall effect on the observed FT values [$F(3, 42) = 4.937, P = 0.005$]. Pairwise comparisons showed a significant difference in FT between different types of path (averaging over trials with gain = 0.7, 1.3, 1.0, or darkness; Fig. S1 *B* and *C*). For the translation gains, the path used had an overall effect on the observed FD values [$F(3.037, 42.517) = 5.747, P = 0.02$, Greenhouse-Geisser corrected for failure of sphericity]. Pairwise comparisons showed significant differences in FD between different types of path (averaging over trials with gain = 0.7, 1.3, 1.0, or darkness; Fig. S1 *B* and *C*).

**Effect of Adaptation to Visual Gain of 1.3 on Triangle Completion in Darkness.** A further 20 participants (age range 21–50, 10 male and 10 female) performed the same adaptation experiment as in experiment 2, but with a rotation gain of 1.3 during the adaptation phase. However, participants' FTs during the instructed turn and sound localization phase post adaptation did not exhibit a significant adaptation in response to the gain manipulation. A 2 × 3 repeated-measures ANOVA on the instructed turn FTs with factors experimental phase (before and after adaptation) and path (see Fig. S2*A* for turn angles) showed no main effect of phase but a main effect of turn angle [$F(1, 19) = 1.926, P = 0.181$ and $F(2, 38) = 46.182, P < 0.001$, respectively]. A similar ANOVA on the sound localization FTs also showed no main effect of phase but a main effect of path [$F(1, 19) = 0.237, P = 0.632, F(2, 38) = 61.459, P < 0.001$; Fig. S2*B*]. Participant debriefs showed that 6 of 20 participants reported feeling dizzy during the experiment with 1.3 rotational gain, compared with none when the rotational gain was 0.7. Thus, we concluded that the 1.3 gain manipulation failed to cause reliable amounts of adaptation. The increased visual motion with a gain of 1.3 may have been enough to prevent a feeling of immersion within a static world, thus preventing recalibration of the interoceptive representation.

Nevertheless, using the responses in the instructed turns task, one can predict how each participant should respond in the navigation task in darkness, postadaptation, according to the MMR model (see main text). Although there were no overall effects of adaptation in this experiment that were reliable across participants, the predicted FTs closely matched the FTs observed in each participant (Figs. S2*C* and S3).

**Further Control Trials in Experiment 2.** In addition to the Dark After condition, following adaptation, three control conditions were also performed when the adaptation gain was 0.7 as well as 1.3.

**Temporal Delay Trials.** Egocentric interoceptive representations are thought to be transient, whereas explicit visual imagery is implicated in long-term memory (1, 2). To investigate whether the relative influences of visual imagery/MMR and interoceptive representations might vary with delay, we included a condition in which participants waited at the end of the outbound path for 10 s before returning. We found no significant effect of this manipulation for either gain manipulation (Fig. S4), which suggests

that responses are either dominated by the MMR rather than any interoceptive representations, or that both types of representation do not decay differentially over 10 s.

**Distraction Digits and Word Trials.** To investigate how distraction affects participants' navigation performance, two conditions recruiting differing levels of distraction were used.

During distraction digit trials, digits from 0 to 99 appeared on screen in a random location and order at 1-Hz frequency. This occurred during the leading and return phase of the triangle completion task. Participants were required to read the numbers out loud throughout the triangle completion task (i.e., during outbound and return paths). No other visual stimuli were available to participants.

In the distraction word trials, 196 common words referring to manipulable objects appeared in the middle of the screen at 1-Hz frequency. In the gain 0.7 condition, words of one to four syllables were used. In the gain 1.3 condition, only monosyllabic words were used.

Fig. S4 shows that FT measures were increased during distraction trials under both gain manipulations. Repeated-measures ANOVA on factors path and trial type showed main effects of both distraction trials, as well as for both gain manipulations [$F(2, 38) = 47.191, P < 0.001, F(3, 57) = 39.587, P < 0.001$, for gain = 0.7 and $F(2, 38) = 56.421, P < 0.001, F(3, 57) = 10.941, P < 0.001$ for gain = 1.3]. Bonferroni-corrected pairwise comparisons show significant differences between distraction (digits) and Dark After FTs as well as between distraction (words) and Dark After FTs for both gain conditions (Fig. S4). This finding may indicate a generalized effect of distraction, in which the record of the turn in the outbound path is weakened, leading to overturning to the origin on the return.

**Subject Debrief Questions for Experiment 1.**

1. How difficult would you rate the task?
2. Were all paths just as difficult?
3. Did you use a particular strategy and did that strategy change over the course of the experiment?
4. If you used more than one strategy, which strategy did you think was the most effective? Did you think it depended on the type of path?
5. If you can remember incidences when you didn't perform so well, can you explain why?
6. At any point in the experiment, did you know where you were in the actual room?

**Subject Debrief Questions for Experiment 2.**

1. Did you use a particular strategy for the rotation to the sound and the rotate a certain angle trials?
2. What strategy did you use when walking in the dark to go back to the origin?
3. Did your strategy change with one of the distractor tasks, such as the eye movement or sound trial?
4. If you can remember incidences when you didn't perform so well, can you explain why?
5. At any point in the experiment, did you know where you were in the actual room?
6. Any other comments?

1. Milner AD, Paulignan Y, Dijkerman HC, Michel F, Jeannerod M (1999) A paradoxical improvement of misreaching in optic ataxia: New evidence for two separate neural systems for visual localization. *Proc Biol Sci* 266:2225–2229.

2. Byrne P, Becker S, Burgess N (2007) Remembering the past and imagining the future: A neural model of spatial memory and imagery. *Psychol Rev* 114:340–375.
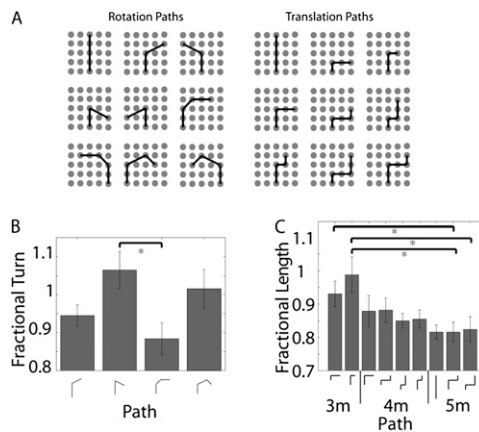
**Fig. S1.** (*A*) Paths used in the rotation and translation gain conditions of experiment 1. Background grid indicates a 1-m scale. (*B*) Fraction of correct turn to the origin along different paths for the rotational gain manipulation. (*C*) Fraction of correct length to the origin along different paths for the translational gain manipulation. FTs and fractional lengths are averaged over the four conditions: gain = 0.7, 1.3, 1.0, or darkness.
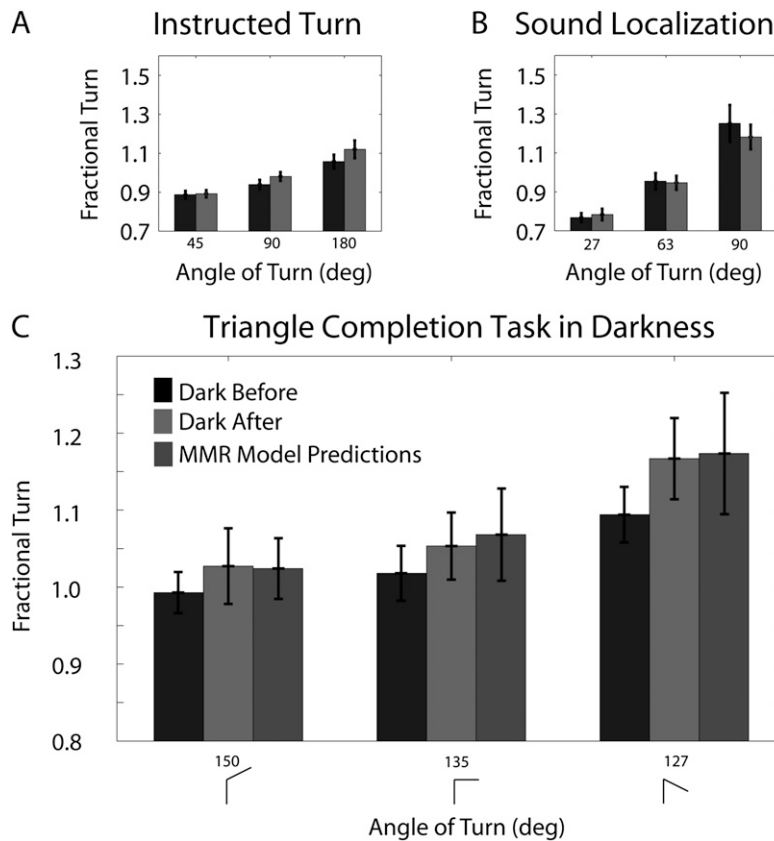


**Fig. S2.** The effect of adaptation to a visual rotational gain of 1.3: adaptation was not reliably found across participants, but individual responses matched the predictions of the MMR model. (*A*) FT values before and after the adaptation phase when participants were instructed to rotate one of three angles. (*B*) FT values before and after the adaptation phase when participants rotated to face a sound at one of three locations. No reliable effects of adaptation were found in *A* or *B*. (*C*) FTs when performing triangle completion entirely in darkness before and after the adaptation phase, shown individually for the three paths. Also shown are the FTs predicted for each participant, based on the MMR model and the reference turns in *A*. Numbers on the *x* axes indicate the actual turn angles of the outbound paths taken. Dark Before and Dark After correspond to phases 1 and 4 of the experiment for *A* and *B*, and phases 2 and 5 for *C*.
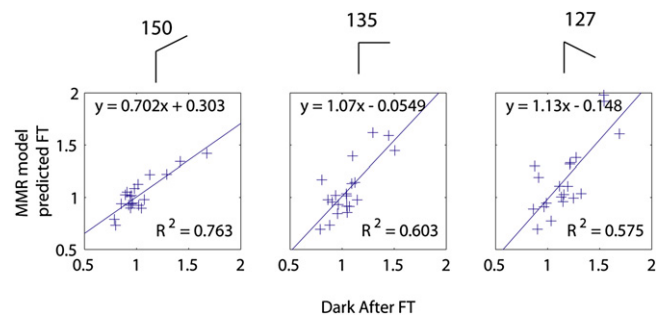
**Fig. S3.** Regression of MMR model predicted FTs against actual FTs in the Dark After condition when adaptation gain is 1.3. The outbound paths are indicated above each graph with the corresponding true turn required to return to the origin.
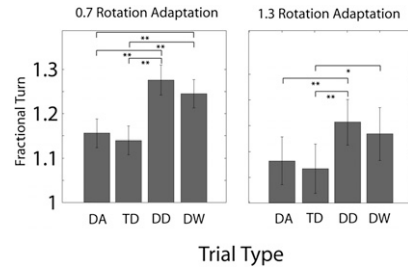


**Fig. S4.** FT measures for the three control conditions (after adaptation) and the Dark After (DA) condition, collapsed across all three types of path. DD, distraction digits; TD, time delay; DW, distraction word conditions. Responses for both adaptation manipulations are shown. Significant pairwise comparisons (Bonferroni corrected) are shown with horizontal lines. $*P \leq 0.05$; $**P \leq 0.01$.