

The brain weights body-based cues higher than vision when estimating walked distances

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Keywords: cue-weighting, distance estimation, human, locomotion, multimodal integration, optic flow, real world

Abstract

Optic flow is the stream of retinal information generated when an observer's body, head or eyes move relative to their environment, and it plays a defining role in many influential theories of active perception. Traditionally, studies of optic flow have used artificially generated flow in the absence of the body-based cues typically coincident with self-motion (e.g. proprioceptive, efference copy, and vestibular). While optic flow alone can be used to judge the direction, speed and magnitude of self-motion, little is known about the precise extent to which it is used during natural locomotor behaviours such as walking. In this study, walked distances were estimated in an open outdoor environment. This study employed two novel complementary techniques to dissociate the contributions of optic flow from body-based cues when estimating distance travelled in a flat, open, outdoor environment void of distinct proximal visual landmarks. First, lenses were used to magnify or minify the visual environment. Second, two walked distances were presented in succession and were either the same or different in magnitude; vision was either present or absent in each. A computational model was developed based on the results of both experiments. Highly convergent cue-weighting values were observed, indicating that the brain consistently weighted body-based cues about twice as high as optic flow, the combination of the two cues being additive. The current experiments represent some of the first to isolate and quantify the contributions of optic flow during natural human locomotor behaviour.

Introduction

In order to effectively navigate throughout the environment, one must be able to process the spatial and temporal properties of environmental features as well as egocentric movement characteristics (Gibson, 1950; Lee, 1976; Warren & Hannon, 1988; Howard & Rogers, 1995; Sun & Frost, 1998). This is achieved using a combination of sensory information, including dynamic visual cues (i.e. optic flow; Gibson, 1950) and body-based information mainly provided by proprioceptive (Mittelstaedt & Mittelstaedt, 2001), efference copy and vestibular cues (Israël & Berthoz, 1989; Harris *et al.*, 2000).

Traditionally, studies investigating the role of optic flow during self-motion perception have presented observers with computer-simulated flow in the complete absence of physical movement. Such studies have shown that optic flow alone can be used to estimate egocentric direction (Warren & Hannon, 1988), speed (Larish & Flach, 1990) and time-to-collision (Lee, 1976). However, little is known about the precise extent to which it is used during natural locomotor behaviours. Of the studies examining optic flow during walking, most have focused on its role for heading perception (Rushton *et al.*, 1998; Warren *et al.*, 2001; Bruggeman *et al.*, 2007).

One of the most important components of self-motion perception is the ability to estimate the extent of a distance travelled. Computer-simulated optic flow alone (e.g. cloud of dots or textured ground plane) has been shown to be sufficient for judging the relative difference between travelled distances (Bremmer & Lappe, 1999; Harris *et al.*, 2000; Redlick *et al.*, 2001; Frenz *et al.*, 2003; Sun *et al.*, 2004a). However, in order to perceive absolute distances travelled, optic flow must be calibrated by other depth cues and it is therefore important to study it further within natural, cue-rich contexts (Sun *et al.*, 2004b).

Body-based cues have also been shown to be sufficient for performing a number of different spatial tasks in the absence of vision. It has been well documented that humans are highly accurate when asked to view a static visual target in the distance and subsequently walk to it blindfolded (Thomson, 1983; Elliott, 1986; Steenhuis & Goodale, 1988; Rieser *et al.*, 1990; Loomis *et al.*, 1992; Mittelstaedt & Mittelstaedt, 2001; Sun *et al.*, 2004b). Humans are also able to estimate distance information when both learning and responding through blindfolded walking (Klatzky *et al.*, 1998; Mittelstaedt & Mittelstaedt, 2001; Sun *et al.*, 2004b), and to some extent when being passively transported (Israël & Berthoz, 1989; Harris *et al.*, 2000; Siegle *et al.*, 2009).

Although optic flow and body-based cues are now known to be independently sufficient for perceiving the extent of travelled distances, this does not directly address issues related to how the

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Received 25 September 2009, revised 27 January 2010, accepted 28 January 2010

brain uses and integrates these cues when both are available. Recent behavioural and neurophysiological research has now provided evidence that the brain typically combines multiple sources of redundant sensory information in a statistically optimal fashion as a function of their relative reliabilities (e.g. Ernst & Banks, 2002; Alais & Burr, 2004; Calvert *et al.*, 2004; Ernst & Bulthoff, 2004). This has also been shown specifically for the integration of visual and vestibular cues during passive self-motion perception in humans and nonhuman primates (e.g. Gu *et al.*, 2008; Butler *et al.*, 2009; Fetsch *et al.*, 2009). Because optic flow is tightly coupled with body-based cues during natural walking behaviours, it is difficult to dissociate (Rieser *et al.*, 1995) and quantify the relative contributions of each, particularly in a real-world setting. The current study employed two complementary techniques to dissociate the contributions of optic flow from those of body-based cues when estimating distances travelled in an open, outdoor environment.

Experiment 1

In order to obtain the relative weighting of optic flow and body-based cues during walking, we first manipulated the visual scale of the environment using spectacle-mounted optical lenses. Three pairs of optical lenses were used: 2.0 \times lenses which created an optically specified magnification, 0.5 \times lenses which created an optically specified minification and 1.0 \times lenses which did not modify the scale of the visual scene. By examining participants' estimates, we were able to evaluate the relative influence of visual and body-based cues by assessing the extent to which the optical manipulations (OMs) affected walked distance estimation.

Materials and methods

Participants

Twenty undergraduate students (10 female) from McMaster University participated in this experiment. Participants either received course credit or monetary compensation of \$10 per hour. Participants ranged in age from 17 to 25 years, had normal or corrected-to-normal visual acuity, and had little or no prior experience with the testing location. All participants provided informed written consent. This research was approved by the Human Ethics Review Board of McMaster University and in accordance the 1964 Declaration of Helsinki.

Stimulus materials

This experiment took place in the centre of a large, open, outdoor field, $\sim 200 \times 150$ m in size (see photo in Fig. 1). The ground was flat with no tactile landmarks and no distinct visual landmarks nearby. The grassy field was surrounded by an oval-shaped paved road with houses and a wooded area around the far perimeter of the road. Three pairs of binocular, Galilean, spectacle-mounted lenses (2.0 \times , 0.5 \times and 1.0 \times) were used (Eschenbach, MaxTV, Ridgefield, CT, USA). Each objective lens was focusable to compensate for $\pm 3D$ of spherical correction or to allow for the adjustment of focal length from 10 ft (~ 3 m) to infinity. All spectacle-mounted lenses were draped with an opaque black cloth which restricted the visual information to only that accessed through the lenses. Participants always wore a set of lenses throughout the entire experiment so that, when no OM occurred (i.e. the wearing of the magnifying or minifying lenses), participants continued to wear the 1.0 \times lenses. Across trials, the order of the OMs was completely randomized in such a way that adaptation effects would be unlikely and participants would be unable to anticipate when

a particular OM would occur. The number of times one particular OM occurred during the stimulus phase, response phase or both, was equalized. Participants were engaged in conversation during walking to ensure that they could not reliably use explicit step counting strategies and were also specifically instructed not to use this strategy.

A questionnaire was administered to the participants after they completed the experiment as a way of gauging the extent to which they were consciously aware of the magnitude of the manipulations. Only one participant correctly guessed how many levels of OMs were used (three levels), while the remaining participants guessed between four and six levels. All participants recognized that the visual information was magnified and/or minimized at some point during the experiment but no participant was able to accurately estimate by how much. When asked how difficult the task was on a scale ranging from 1 (very easy) to 10 (very difficult), it was rated a 5 on average.

Procedure

Participants were required to first view an in-depth stationary target positioned at a particular distance (6, 8, 10 or 12 m), then turn 180 $^\circ$ and reproduce this distance by walking the equivalent extent in the opposite direction (See Fig. 1 for an illustration of the task). The distance walked thus reflects the contributions of each of the inputs (optic flow and body-based cues) used to match to the spatial extent perceived during the visual preview. The OM occurred either during the static visual preview phase alone (OM_{view}) or during both the static visual preview phase and the walking phase (OM_{view+walk}) with the same OM occurring in both phases. The OM_{view} served as an important control condition through which the specific effects of the lenses on the static visual information could be quantified. The most interesting findings, however, come from comparing the results of the OM_{view} condition with those of the OM_{view+walk} condition, considering that the main objective of this study was to specifically evaluate the extent to which dynamic visual cues and body-based cues were weighted during walking.

Results

A four (distance: 6, 8, 10, 12 m) \times three (OM: 0.5 \times , 1.0 \times , 2.0 \times) repeated-measures ANOVA was conducted on participants' average estimates (across two repetitions) for both conditions. Planned contrasts were conducted as a way of comparing the estimates of the two OMs (2.0 \times and 0.5 \times) to those for which no manipulation of visual cues occurred (1.0 \times).

In the OM_{view+walk} condition, if participants were exclusively using optic flow information during the walking phase, any effect of the lenses during the static visual preview should be cancelled out in the response phase, thus resulting in no observable differences in distance estimates between the different OMs. This is because, when participants wore the same lenses in both phases, the visual information within the same spatial range during the visual preview and during the walking phase would be identical (e.g. same amount of texture on the ground, etc.). If, however, participants were exclusively using body-based cues during the walking phase, the predicted OM-related effects in the OM_{view+walk} condition would be of the same magnitude as those observed for the OM_{view} condition. Applying this logic, we can calculate the weighting of dynamic visual cues and body-based cues during walking.

For the OM_{view} condition, because participants were initially forced to estimate the distance from a stationary viewpoint by relying entirely on vision (magnified, minified or unaltered), these responses were used to quantify the maximal perceptual effects of the lenses. The

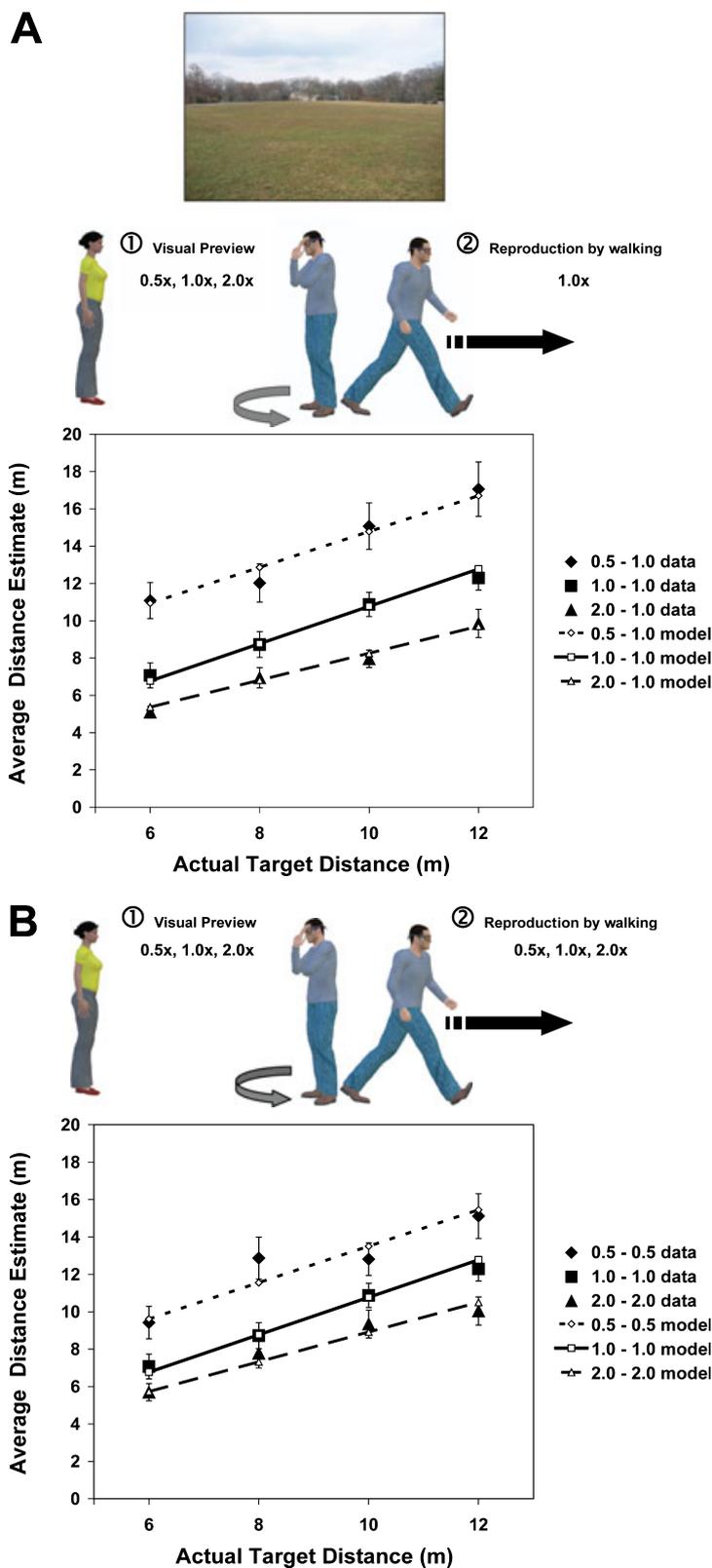


FIG. 1. Methods and results for experiment 1: magnification and minification lenses. (A1 and B1) Participants first viewed a target positioned directly in front of them at a distance of 6, 8, 10 or 12 m in an open, outdoor field (inset photo). (A2 and B2) They were then asked to reproduce this distance by walking in the opposite direction. Magnification and minification lenses were worn either (A) during the initial viewing of the target, OM_{view} or (B) during both the initial viewing and the walking phase, $OM_{view+walk}$. (A, graph) Average distance estimates for OM_{view} . (B, graph) Average distance estimates for $OM_{view+walk}$. Error bars represent SEM. The solid markers represent the actual average data values and the open markers connected by the lines represent the model predictions. The values in the legend indicate the magnification factors of the lenses used in stimulus and response phases.

results indicate that, when wearing the 2.0x lenses, participants significantly undershot the target distance on average compared to the 1.0x trials ($M_{OMview_2.0x} = 76\%$; $F_{1,19} = 43.74$, $P < 0.001$), while the 0.5x lenses resulted in a significant overshoot of the target distance ($M_{OMview_0.5x} = 143\%$; $F_{1,19} = 32.39$, $P < 0.001$; Fig. 1A). There-

fore, when participants were required to judge distances using static visual cues alone, their estimates revealed effects of the OMs in the predicted directions. These results are similar to findings previously reported when observers estimated static distances when wearing a monocular low-vision telescope (Shah & Sedgwick, 2004) and when

computer-generated visuals were minified through software (Kuhl *et al.*, 2006).

A similar, yet notably distinct, trend of results was found for the $OM_{\text{view+walk}}$ condition. When wearing the 2.0 \times lenses, participants significantly undershot the target distance compared to when wearing the 1.0 \times lenses ($M_{OM_{\text{view+walk}}\ 2.0\times} = 84\%$; $F_{1,19} = 12.19$, $P < 0.01$), while the 0.5 \times lenses resulted in a significant overshoot of the target distance ($M_{OM_{\text{view+walk}}\ 0.5\times} = 130\%$; $F_{1,19} = 32.50$, $P < 0.001$; Fig. 1B). However, importantly, the extent of the over- or undershoots in the $OM_{\text{view+walk}}$ condition were not as great as those observed in the OM_{view} condition (2.0 \times , $F_{1,19} = 4.42$, $P < 0.05$; and 0.5 \times , $F_{1,19} = 9.79$, $P < 0.01$).

In order to quantify the weighting of optic flow and body-based cues, a mathematical model containing an explicit weight parameter was fitted to the entire data set. When participants viewed the target for a given trial, τ , they formed a visual percept of the static distance (D_{vps}) given by

$$D_{\text{vps}}(\tau) = c_m D_s(\tau) + c'_m \quad (1)$$

where $D_s(\tau)$ is the static distance presented, and c_m and c'_m are constants that depend on the OM, $m \in \{1.0\times, 2.0\times, 0.5\times\}$. Furthermore, $c_{1.0\times}$ and $c'_{1.0\times}$ were set to equal one and zero, respectively, as we assume that participants form an approximately accurate perception of $D_s(\tau)$ when the viewing magnification is 1.0 \times . This assumption is based on the fact that, under full visual conditions, it has been demonstrated that observers are able to accurately perform several different visually-directed action tasks. These have included walking blindfolded to a previously viewed target (Thomson, 1983; Elliott, 1986; Steenhuis & Goodale, 1988; Rieser *et al.*, 1990; Loomis *et al.*, 1992; Mittelstaedt & Mittelstaedt, 2001; Sun *et al.*, 2004b), continuously pointing to a previously viewed target when walking along direct and indirect paths in the absence of vision (Loomis *et al.*, 1992; Campos *et al.*, 2009), and throwing objects to previously viewed targets in the absence of vision (Sahm *et al.*, 2005). See Loomis & Philbeck (2008) for a thorough review of this extensive literature on distance perception. Although the form we have chosen for $D_{\text{vps}}(\tau)$ is probably not valid over all distances possible, from the fit results shown in Fig. 1 it is clear that it provides an excellent approximation for the range of distances considered here.

After forming a visual distance-to-target estimate, participants then walked until their perceived walked distance matched this distance estimate. Participants' multisensory percept of walked distance (D_{mpw}) for trial τ can be approximated by

$$D_{\text{mpw}}(\tau) = (w_V D_{\text{vpw}}(\tau) + (1 - w_V) D_{\text{bpw}}(\tau)) \quad (2)$$

where $w_V \in [0, 1]$ is the weighting of dynamic visual cues (optic flow), and D_{vpw} and D_{bpw} are independent estimates obtained from visual perception of walked distance and body-based perception of walked distance, respectively. We assume that the magnifying lenses affected visual processing during walking in the same way that they affected the processing of static visual distances. In addition, we also assume that the body-based estimate of the walked distance is essentially accurate (apart from random noise; Loomis & Philbeck, 2008). Thus, if $D_w(\tau)$ is the actual walked distance presented on trial τ , then $D_{\text{vpw}}(\tau) = c_m D_w(\tau) + c'_m$ and $D_{\text{bpw}}(\tau) = D_w(\tau)$. Here we treat perception of travelled distance as a linear process, mostly because, relative to the effect of optical manipulations, any effect of non-linearity would be very small. It is important to note that past evidence has shown that the perception of travelled distance experienced through optic flow alone exhibits evidence of a leaky

spatial integrator for longer distances (i.e. > 12 m; Lappe *et al.*, 2007). However, this probably does not contribute significantly to the current data considering that shorter distances were tested here. Further, how this leaky integrator exhibits itself when optic flow is combined with body-based cues is currently not known and would be an interesting future question.

By equating expressions for the visually perceived static target distance, $D_{\text{vps}}(\tau)$ (Equation 1) with the walked distance percept, $D_{\text{mpw}}(\tau)$ (Equation 2), $D_w(\tau)$ can be solved for in terms of the actual static target distance, $D_s(\tau)$. This results in:

$$D_w(\tau, i) = \begin{cases} D_s(\tau) + a_i & \text{view and walk : 1.0}\times \\ c_{2.0\times/0.5\times} D_s(\tau) + c'_{2.0\times/0.5\times} + a_i & \text{view : 2.0}\times \text{ or } 0.5\times, \text{ and walk : 1.0}\times \\ \frac{c_{2.0\times/0.5\times} D_s(\tau) + (1 - w_V) c'_{2.0\times/0.5\times}}{w_V (c_{2.0\times/0.5\times} - 1) + 1} + a_i & \text{both view and walk : 2.0}\times \text{ or } 0.5\times \end{cases} \quad (3)$$

where a_i is a constant that has been added to account for any systematic error that might exist for participant i . See Supporting information, Appendix S1, for derivation of Equation 3 for $OM_{\text{view+walk}}$ trials.

In creating the model, we assumed that, without an OM, both the estimate of the static visual distance and the estimate of the walked distance are accurate. However, each percept alone does not necessarily have to be accurate. Even if there is a bias, as long as the biases in the perception of the static target distance and the walked distance are in the same direction and of the same magnitude, the logic holds. If the perception of the stimulus is not accurate, the brain may have still learned to produce an adaptive response. Consequently, the final outcome of the task would exhibit accurate estimates. In fact, accurate estimates have been demonstrated extensively through many studies using the blind-walking task, one study using a sighted walking task (Sun *et al.*, 2004a,b) and importantly, the current results for the 1.0 \times view–1.0 \times walk condition. More importantly, even if the performances on these tasks are not highly accurate, the magnitude of errors observed were much smaller than those observed for the main manipulations (i.e. the 2.0 \times and 0.5 \times OMs) and the relation between perception and stimulus distance revealed through the model should be independent of the errors created due to the OM.

Clearly this method of accounting for systematic participant-specific biases is not logical as the target distance approaches zero, but it provides an excellent approximation over the range of our data. For clarity, we provide a more explicit derivation of the third line of Equation 3 in the Appendix section. If Equation 3 models the behaviour of participants up to an additive Gaussian noise term, then this model can be fitted to our entire dataset (one average distance estimate per participant, per condition = 400 points) using standard maximum-likelihood-least-squares procedures. The fitted model, which accounted for a large proportion of the data variance ($R^2 = 0.75$), is shown along with the original experimental data in Fig. 1. The resulting optic flow weight was found to be $w_V = 0.328$, and thus the weighting for body-based cues was found to be $w_B = 1 - w_V = 0.672$, indicating that body-based cues dominated the combined estimate during walked distances. Likelihood ratio tests confirmed that w_V was significantly greater than zero ($P = 0.0003$), highlighting the contributions of optic flow, and w_V was significantly < 0.5 ($P = 0.021$), indicating its lesser role compared to body-based cues. The remaining parameters took on values of $c_{2.0\times} = 0.723$, $c_{0.5\times} = 0.960$, $c'_{2.0\times} = 0.259$, $c'_{0.5\times} = 4.41$, while the mean value of a_i across participants was found to be $\bar{a}_i = 0.773$ m.

A wealth of multisensory research, including many studies using cue-conflict approaches, have demonstrated that when different sources of sensory information are combined the brain weights the more reliable cue higher than the less reliable cue (e.g. Ernst & Banks, 2002). Although cue-conflict approaches are extremely valuable there is sometimes the concern that, when creating cue-conflicts, relative cue-weighting values may simply reflect a unique effect of the stimulus manipulation itself rather than a generalizable, naturally occurring phenomenon. For instance, in the case of the current study, an initial concern might be that in the process of generating cue conflicts through manipulating the visuals, the optic flow cues in experiment 1 might be perceived to be less reliable and thus weighted less. While this remains a possibility, other arguments could be made as to why this is less of a concern here. In the $OM_{\text{view+walk}}$ condition, the static visual information present during the visual preview, although distorted relative to the real environment, included information that was necessary for participants to be able to direct their actions during the walked response. Because the visual information was identically manipulated in the response phase, this decreases the likelihood that the visuals would be discounted, considering that, in relative terms, they remained unchanged.

In order to further highlight the significance of the $OM_{\text{view+walk}}$ condition in this regards, we can consider an additional condition that was conducted in which the OM only occurred during the walking phase (OM_{walk}). In this condition, results showed that participants' estimates were approximately equal across the different OMs, indicating that the responses were not affected by either the magnifying or the minifying lenses. Unlike the $OM_{\text{view+walk}}$ condition, in the OM_{walk} condition visual information was only manipulated during the walking phase and therefore it was of a different scale than that experienced during the visual preview. Consequently, for this condition, the dynamic visual information during walking might have been weighted much lower simply because of the significantly different visual scale between preview and subsequent walking phase and the resultant difficulty in making an accurate comparison across two different scales. A strategy of exclusively using body-based cues in this case might therefore have been advantageous due to the unreliable, obviously changing, visual information. Supporting this suggestion is evidence from the abovementioned blind-walking studies demonstrating that observers can very effectively reproduce a previously viewed target distance when walking in the complete absence of continuously updated visuals. These concerns with the OM_{walk} condition, therefore, serve to further highlight the necessity of focusing on the results of the $OM_{\text{view+walk}}$ condition. To further verify the results of Experiment 1, we also conducted a control experiment (see Experiment S1 in supporting Appendix S2).

Having considered these arguments, it is important to note that, even with the use of the $OM_{\text{view+walk}}$ condition, it remains possible that the fact that visual information was frequently changed relative to body-based cues, or that the visuals were obviously distorted relative to the known scale of the real environment, may have globally down-weighted visual information. Therefore, in order to further verify our findings and to help disambiguate the cause for the higher weighting of body-based cues, we developed a second approach to evaluate relative cue-weighting under conditions in which the veridicality or quality of the visual information remained unchanged and the natural relation between dynamic visual information and body-based cues was maintained. This was achieved by creating a cue-dissociation over two successive stimulus presentations (Ellard & Shaughnessy, 2003) in order to assess the additional influence of optic flow over body-based cues alone during walking.

Experiment 2

In experiment 2, participants were told that they would experience a travelled distance twice by walking and would subsequently be required to produce an estimate of this distance by adjusting a visual target until the egocentric, self-to-target distance matched the distance they initially walked. For the majority of the trials the two stimulus distances were identical; however, for a subset of trials the two stimulus distances actually differed by 2 m unbeknownst to the participants. In order to quantify the additional influences provided by optic flow we compared two modes of distance presentations involving different combinations of sensory information: body-based cues only and body-based cues plus vision.

Materials and methods

Participants

Eighteen undergraduate and graduate students (nine female) with ages ranging from 18 to 36 years participated in this study. All participants had normal or corrected-to-normal vision. All participants received either course credit or payment for their participation, were naive to the aims of the study, and had little or no prior experience with the testing location. Each participant completed two 1-h sessions on different days. All participants provided informed written consent. This research was performed in accordance with the ethical standards specified by the Human Ethics Review Board of McMaster University and the 1964 Declaration of Helsinki.

Stimulus materials

This experiment took place in the same open outdoor field as Experiment 1. Industrial earmuffs were worn to control for any environmental auditory localization cues. In the conditions in which participants were required to walk without vision, black opaque safety goggles were worn to eliminate all visual and directional light cues. Stimulus distances (8, 10, 12 and 14 m) were pre-measured and discretely marked with coloured golf tees, which were not visible to participants throughout the experiment. One of the experimenters served as an adjustable target during the response. Responses were measured using a retractable tape measure.

Procedure

Participants were always blindfolded before being guided to the starting position of each trial and five predetermined starting positions were used in a random order. They were asked not to count their steps during walking and were also engaged in conversation during walking. Participants learned two walked stimulus distances in succession, which they were led to believe were identical in magnitude (See Fig. 2A for an illustration of the task). They were first presented with one distance interval by walking until verbally instructed to stop, turned 180° and were then presented with the second distance interval until instructed to stop. When two distances were presented in a sequential manner, it is possible that there were within-participant and between-participants variations in terms of the weight assigned to a particular distance (first or second distance). However, by having a full factorial design including all possible cue combinations and distance presentation orders, we were able to isolate the effect of cue from the effect of order.

Subsequently, participants were asked to reproduce the learned distance by verbally instructing the experimenter to move in-depth, until the egocentric distance between the participant and the experimenter matched the distance originally walked (method of adjustment). When adjusting the position of the experimenter, for half of the

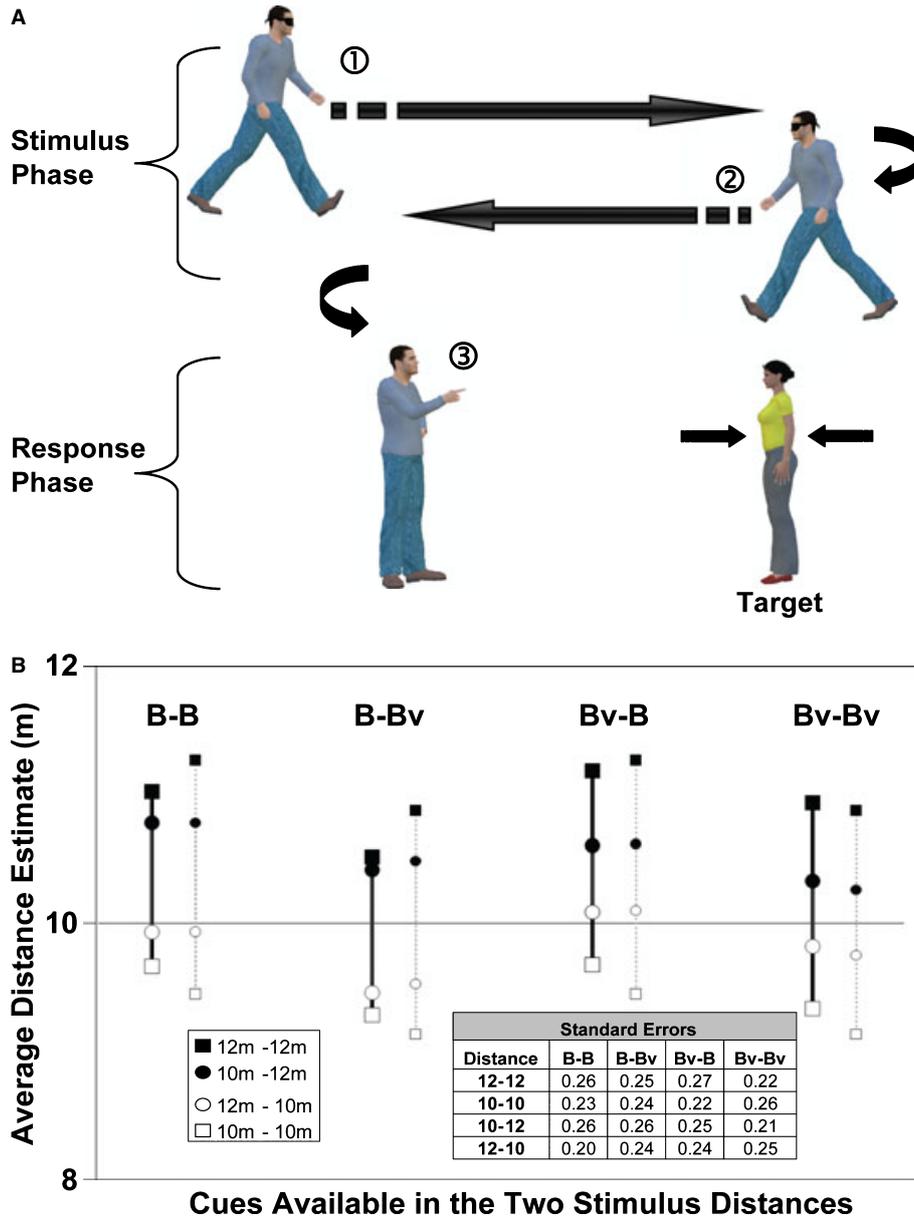


FIG. 2. Methods and results for experiment 2: cue conflict over consecutive trials. (A) Participants first experienced one distance interval by walking until asked to stop (1). They turned 180° and walked a second distance interval until again asked to stop (2). From this stationary position, they then adjusted the target either towards or away from themselves until their visual self-to-target distance matched the distance they had walked previously (3). For most trials, 1 and 2 were congruent, but for a subset of the trials they differed in magnitude. Visual information was either present in phase 1 only (Bv–B), phase 2 only (B–Bv), both phase 1 and phase 2 (Bv–Bv), or neither (B–B). The B–B condition is illustrated here. (B) Average estimates for each of the four conditions comparing discrepant distance estimates (circles) to congruent distance estimates (squares) are represented by the larger symbols connected by the solid lines. Average values as predicted by the mathematical model for each of the four conditions are represented by the smaller symbols connected by the dotted lines and are positioned to the right of the actual data. The figure legends specify the distance walked in the two stimulus distances and the table summarizes the standard error values from the observed data for each condition and each distance pair.

trials the experimenter moved away from the participant and for the other half of the trials the experimenter moved towards the participant.

In 60% of the trials the two stimulus distances were identical (congruent distance trials; i.e. 8–8, 10–10, 12–12 and 14–14 m). However, unbeknownst to the participants, in 40% of the trials the two stimulus distances actually differed by 2 m (discrepant distance trials; 10–12 and 12–10 m). In order to quantify the additional influences provided by optic flow we compared two modes of stimulus distance presentation involving different combinations of sensory information: body-based cues alone (B; i.e. blind-walking) and body-based cues

plus vision (Bv; i.e. sighted walking). A full permutation of the two stimulus distance modes was included, resulting in four cue conditions: B–B, B–Bv, Bv–B and Bv–Bv. This comprehensive design allowed us to evaluate the independent effects of cue and of distance presentation order.

An informal survey of participants following their participation indicated that they were unaware of the distance discrepancy. No participants spontaneously reported that they noticed any differences between the two distances and this was also true when explicitly prompted.

Results

For the congruent distance trials, it was found that there were slight underestimations in the responses. Furthermore, when optic flow was available in the second distance, participants underestimated distance to a significantly greater degree than when it was absent. This was revealed through a significantly greater underestimation in the B–Bv than the B–B condition ($F_{1,35} = 11.73$, $P < 0.01$) and for the Bv–Bv than the Bv–B ($F_{1,35} = 6.66$, $P < 0.05$). In order to reveal the effects attributable to the addition of optic flow, we examined the distance estimates produced during the discrepant distance trials. Because optic flow alone cannot be isolated in this case, we must evaluate the additional effects of having optic flow during walking compared to walking in the absence of vision. If optic flow had no modulating effects on distance perception, the weighting of the two stimulus distances would not be affected by the availability of optic flow. If, however, one of the two cue conditions was weighted higher or lower, we would expect to see participants' estimates vary accordingly across conditions.

The results for the discrepant distance trials allowed us to calculate the relative weighting of each of the two stimulus distances by determining where the discrepant distance estimates fell relative to the congruent distance estimates. Such effects were explored by differentiating the effects of order (e.g. 10–12 m vs. 12–10 m) from the effects of the presence or absence of optic flow (e.g. B–B vs. Bv–B). Figure 2B illustrates the average estimates for the relevant congruent distance trials (i.e. 10–10 and 12–12 m) and the average estimates for both discrepant distance trials (10–12 and 12–10 m) for each cue condition.

In terms of the effect of distance presentation order across all conditions, estimates for trials in which the 10-m interval was presented second (12–10 m) were shorter than estimates for trials in which the 12-m interval was presented second (10–12 m): B–B, $t_{71} = 3.72$, $P < 0.000$; B–Bv, $t_{71} = 4.82$, $P < 0.001$; Bv–B, $t_{71} = 2.34$, $P < 0.05$; Bv–Bv, $t_{71} = 2.25$, $P < 0.05$. This result indicates that participants were not simply taking a weighted average of the two distances presented and that the second stimulus distance was given a higher weighting than the first distance (i.e. a recency effect).

In terms of the cue-related effects, when optic flow occurred in the second distance interval its effect was not apparent. The magnitude of the response differences for the two discrepant distance trials (12–10 m vs. 10–12 m) were highly similar regardless whether optic flow was present in the second distance or not. In other words, similar results were observed for the B–B and B–Bv conditions and for the Bv–B and Bv–Bv conditions. However, the modulating effects of optic flow were revealed when comparing its presence and absence in the first distance interval. As shown in Fig. 2B, when examining the two conditions in which optic flow was not available during the first stimulus distance (B–B and B–Bv), a strong recency effect was observed, demonstrated by the large difference between the estimates for 10–12 m and those for 12–10 m. In fact, for each of these two conditions, estimates for the 10–12 m trials (filled circles) were not significantly different from the 12–12 m congruent trials (filled squares), and the estimates for the 12–10 m trials (open circles) were not significantly different from the 10–10 m congruent trials (open squares). In contrast, for the two conditions in which optic flow was available during the first stimulus distance (Bv–B and Bv–Bv), the recency effect was smaller. This was demonstrated by the fact that, in each of these two conditions, the estimates for the 10–12 m trials were significantly shorter than those for the 12–12 m congruent trials (Bv–B, $t(71) = -2.35$, $P < 0.05$; Bv–Bv, $t(71) = -2.55$, $P < 0.05$) and the estimates for the 12–10 m trials were also significantly longer than those for the 10–10 m congruent trials (Bv–B, $t(71) = -1.96$,

$P = 0.05$; Bv–Bv, $t(71) = -2.02$, $P < 0.05$). Taken together, the results of the discrepant distance pairs indicate that, while in general second distances were weighted higher (recency effect), having optic flow in the first distance reduced this order effect.

In order to more precisely examine the relative roles of optic flow and body-based cues, a mathematical model was fitted to the data. The perception of traversed distance based on combined input from the first and the second distance, D_p , can be expressed as

$$D_p = (w_{1,m12}D_1 + (1 - w_{1,m12})D_2) + a_{m12,i}, \quad (4)$$

where $w_{1,m12}$ is a weight parameter for the first distance that depends on the manipulation of cue availability in both the first and second distance presentation (i.e. $m12 \in \{BB, BBv, BvB, BvBv\}$) and D_1 and D_2 are the perception of the first and second traversed distances, respectively. Additionally, $a_{m12,i}$ represents four sets of bias parameters that also depend on cue availability in the first and second distance conditions, and on participant ID , i . As it turns out, all quantitative results that follow would be very nearly identical if we had let the bias parameters depend only on cue availability in the second walked distance. This is consistent with the patterns observed in the raw data means as described above (also see Fig. 2B). Equation 4 was fitted to our entire dataset (one average distance estimate per participant per condition = 288 points) using standard maximum-likelihood-least-squares procedures, as above. The fitted model, which accounted for a large proportion of the data variance ($R^2 = 0.88$), is shown along with the original experimental data in Fig. 2B. Fitted model parameters were found to be: $w_{1,BB} = 0.285$, $w_{1,BBv} = 0.259$, $w_{1,BvB} = 0.371$, $w_{1,BvBv} = 0.372$, $\bar{a}_{BB,i} = -0.647$, $\bar{a}_{BBv,i} = -1.072$, $\bar{a}_{BvB,i} = -0.606$ and $\bar{a}_{BvBv,i} = -0.893$. As expected, the weight values are all < 0.5 , indicating a higher weighting of the second distance presentation in the final response. Moreover, consistent with the participants' mean estimates illustrated in Fig. 2B, the first distance was weighted higher for cases in which optic flow was present in the first distance as opposed to absent in the first distance.

Equation 4 assumes that the brain uses a linear combination of the first and second walked distance estimates (plus some participant-specific biases). Typically, a linear combination of stimulus estimates is seen in the context of Bayesian integration with a uniform prior (e.g. Ernst & Banks, 2002; Alais & Burr, 2004). In this case, each estimate contributes to the linear combination in proportion to its reliability. Thus, assuming that participants' estimates for the first walked distance have a reliability of $1/\sigma_1^2$ when only body-based information is available during that walk, and a reliability of $1/\hat{\sigma}_1^2$ when both vision and body-based cues are available, and using similar definitions for the second distance, then the statistically optimal model weights for the first distance can be written as:

$$w_{1,BB} = \frac{1/\sigma_1^2}{1/\sigma_1^2 + 1/\sigma_2^2}, \quad w_{1,BBv} = \frac{1/\sigma_1^2}{1/\sigma_1^2 + 1/\hat{\sigma}_2^2},$$

$$w_{1,BvB} = \frac{1/\hat{\sigma}_1^2}{1/\hat{\sigma}_1^2 + 1/\sigma_2^2}, \quad w_{1,BvBv} = \frac{1/\hat{\sigma}_1^2}{1/\hat{\sigma}_1^2 + 1/\hat{\sigma}_2^2}. \quad (5)$$

Interestingly, simple algebra shows that these equations are overdetermined in the sense that they must satisfy the relation

$$w_{1,BB}w_{1,BvBv}(1 - w_{1,BBv})(1 - w_{1,BvB}) - w_{1,BBv}w_{1,BvB}(1 - w_{1,BB})(1 - w_{1,BvBv}) = 0. \quad (6)$$

Substituting our fitted weights into the left-hand side of Equation 6 gives a value of 0.0062. In order to determine how likely it would be to obtain a value this close to zero by random chance, we randomly and independently selected 100 000 sets of four weights from the interval [0,1] and used them to calculate 100 000 values of the left-hand side of Equation 6. We found that 7.44% of the resulting values were, in magnitude, ≤ 0.0062 , corresponding to a P -value of 0.074. Thus, using a criterion of $\alpha = 0.05$, we cannot say with statistical certainty that participants were combining the first and second walked distances in a statistically optimal fashion, but we do have a strong trend suggesting this. Given this trend, along with the vast literature supporting the existence of reliability weighting across a wide variety of circumstances, this seems to be a reasonable assumption.

Considering that the brain seems to be performing reliability-weighting between the two walked distances in a given trial of our experiment, it must be able to calculate the reliability of each walked distance estimate (first and second). This information would have to come from the individual reliabilities of the dynamic visual cues and body-based contributions themselves. These values can be calculated explicitly by making similar reliability-weighting assumptions to those above. Thus, if the perception of the first walked distance takes the form of $w_{1V}D_{1V} + (1 - w_{1V})D_{1B}$, when visual information is present in the first walked distance (where D_{1V} and D_{1B} are visual and body-based estimates from the first distance exposure), and the perception of the second distance takes a similar form, then the visual weights w_{1V} and w_{2V} can be calculated (see Appendix for details). The cue-weightings within each distance in the distance pairs work out to be $w_{1V} = 0.37$ (thus $w_{1B} = 0.63$) and $w_{2V} = 0.06$ (thus $w_{2B} = 0.94$). Therefore, consistent with experiment 1, body-based cues trump vision and this pattern of results was true for both the first and the second distances in experiment 2 (see Experiment S2 in supporting Appendix S2).

One of the most interesting and novel aspects of these results is that relative cue-weighting changed over the two stimulus distance presentations. Specifically, the weighting for vision was higher when it was available in the first distance than when it was available in the second distance. Because the sensory information was not distorted and the relation between the two cues remained the same in the two distances, it is highly unlikely that the observed variations in cue-weighting between the first and second stimulus distances reflect differences at a perceptual level. Therefore, the results here show that, although body-based cues are generally weighted higher than optic flow, optic flow information appears to be better preserved over sequential stimulus presentations. Whether these potential memory-related effects are due simply to decay over time, or perhaps the interference of the second distance presentation, is an important future research question. Unlike most multisensory studies that investigate momentary cue integration for discrete stimulus presentations, the current study evaluated cue integration involving sequential stimulus presentations taking place over time. As such, this provides a unique opportunity to understand cue integration as it is affected by differences in cue-specific memory as well as momentary cue reliability.

This experiment reveals the dynamic nature of cue integration. The results call for a more systematic investigation of the mechanisms underlying sensory processing in the context of temporally-contingent cue integration, a common occurrence under natural circumstances. For example, in path integration, observers must integrate information from multiple segments of a travelled route. It is therefore important to precisely understand how individual segments and sensory cues are weighted in this context of sequentially experienced sensory events. To further verify the results of Experiment 2, we also conducted a control experiment.

General discussion

Together these results highlight the importance of body-based cues and the dynamic nature in which optic flow and body-based cues are integrated during one of the most common and critically important tasks performed daily by humans: walking. In doing so, several novel and important findings were illustrated and several unique methodological contributions were introduced. First, the results of both experiments reveal complementary findings that challenge past influential theories that characterized optic flow as an all-inclusive solution to self-motion perception (Gibson, 1950). The results presented here clearly demonstrate that when body-based cues are available during natural locomotor behaviours they can predominate over visual inputs in dynamic spatial tasks that require the integration of information over space and time. It could be the case that body-based cues are particularly well-suited for tasks that require an accumulation of recently acquired information. Further, from an ecological perspective, it makes sense that humans as terrestrial animals should be highly reliant on the rich and stable travelled distance information provided by body-based cues. In fact, animal literature has shown that other terrestrial animals such as ants do in fact rely more strongly on proprioceptive information from leg movements, while flying insects such as honeybees mainly rely on optic flow (see Collett *et al.*, 2006 for a review).

Further, the claims made here regarding relative cue contributions to travelled distance perception are strengthened by the highly similar pattern of results observed in the two experiments. This is particularly true, recognizing the complementary nature of the two approaches with each offering unique advantages for dissociating tightly coupled cues in natural environments. In experiment 1 the cue conflict was created during simultaneously presented sensory information and, because during the $OM_{\text{view+walk}}$ condition the visual information was identical during stimulus and responding, this minimized the chance of causing an unfair bias. In experiment 2 the absolute distance information provided by each cue was the same for each distance travelled, and thus the natural coupling of the two cues was preserved and the quality of both cues was maintained in their truest form. Yet overall, regardless of how the individual contributions of particular cues were dissociated in the two experiments, both lines of evidence support a direct linear combination of optic flow and body-based cues for travelled distance estimation, suggesting that this is a robust phenomenon.

Currently, very little work has explicitly quantified the relative weights of visual and nonvisual cues during full-scale self-motion. Most relevant to the current study are important behavioural and neurophysiological findings that have recently been described in the context of visual-vestibular integration for heading perception (Gu *et al.*, 2008; Butler *et al.*, 2009; Fetsch *et al.*, 2009). Behavioural studies in both humans (Butler *et al.*, 2009; Fetsch *et al.*, 2009) and nonhuman primates (Fetsch *et al.*, 2009), and also neurophysiological studies in nonhuman primates (Gu *et al.*, 2008; Fetsch *et al.*, 2009), now suggest that visual and vestibular information appears to be weighted in a statistically optimal manner. Specifically, it has been shown that both psychophysical measures and neural responses demonstrate a reduction in variance when visual and vestibular cues are combined, compared to unisensory conditions. There is also evidence of a consistent bias towards vestibular cues in the combined cue conditions (Butler *et al.*, 2009; Fetsch *et al.*, 2009). Interestingly, neurons within the dorsal medial superior temporal area, which has traditionally been known to respond preferentially to optic flow (Duffy & Wurtz, 1991; Lappe *et al.*, 1996), have now also been shown to respond during passive self-motion in the complete absence of vision

(i.e. purely vestibular stimulation; Gu *et al.*, 2008; Fetsch *et al.*, 2009). Overall, the results of the current experiments expand on these recent findings by illustrating that the brain also combines body-based cues and optic flow in a statistically optimal fashion during active, self-generated movements (with the added inclusion of proprioception and efference copy information).

Unlike many laboratory-based tasks, this work provides direct and tangible evidence to reveal multisensory integration using a basic, everyday behaviour in a natural, familiar environment, thus allowing for an ecologically valid evaluation of spatial processing during locomotion. Overall, these experiments are the first, to our knowledge, that effectively isolate and, more importantly, quantify the specific contributions of optic flow to travelled distance perception during walking in natural, cue-rich environments. Other investigations have examined the effects of systematically removing different sources of sensory information during navigation (Chance *et al.*, 1998; Kearns *et al.*, 2002; Sun *et al.*, 2004b; Waller *et al.*, 2004). Some, such as Kearns *et al.* (2002), have achieved this using virtual reality (VR); they found that, while participants were able to use optic flow alone to complete a path integration task, the introduction of locomotor cues (proprioceptive and vestibular) led to a decreased variability in performance. Several other studies conducted in virtual reality have varied the relation between visual and body-based cues simultaneously online by manipulating visual gain (i.e. the extent of simulated visual distance travelled as a function of physical distance). This has been done to evaluate the effects of recalibration over time (Durgin *et al.*, 2005; Mohler *et al.*, 2007) and on a discrete trial-by-trial basis (Kearns, 2003) to evaluate relative cue-weighting for travelled distance perception (Campos *et al.*, 2008). For instance, using highly controlled simulation scenarios, Campos *et al.* (2008) have provided further evidence supporting the higher weighting of body-based cues for travelled distance estimation. However, although VR provides a high level of control over stimulus conditions and can create very subtle changes in cue relations, the visual displays used often do not provide important visual cues in their truest form and are known to result in misperceptions of distance (Thompson *et al.*, 2004) and visual speed (Banton *et al.*, 2005). It is for this reason that, when possible, investigating multimodal cue integration during locomotor behaviours in the real world is particularly revealing.

Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Supplementary Model Material: Derivation of Equation 3 for $OM_{\text{view+walk}}$ trials.

Appendix S2. Supplementary Experiment S1 and Supplementary Experiment S2.

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Acknowledgements

We would like to thank George Chan, Daphne Maurer, Suzanna Becker, Jim Lyons and John Butler for their valuable insights and Adrian Brucker, Patricia Freitas, Celia Hsiao, Ashley Towns, Emma Turner, Zeljka Vucetic and Michael Wong for their assistance in collecting the data, and Steven Pong for help with the figures. This research was supported by grants from the Natural Sciences

and Engineering Research Council of Canada (NSERC) and the Canadian Foundation for Innovation (CFI) to H.J.S. and an NSERC fellowship awarded to J.L.C.

Abbreviations

Experiment 1

D_{bpw} , body-based perception of walked distance; D_{mpws} , multisensory perception of walked distance; D_s , static distance presented; D_{vps} , visual perception of static distance; D_{vpws} , visual perception of walked distance; D_{ws} , actual walked distance presented; M, mean; OM_{walk} , OM during walked response phase alone; OM, optical manipulation; OM_{view} , OM during the static visual preview phase alone; $OM_{\text{view+walk}}$, OM during both the static visual preview phase and the walking phase.

Experiment 2

B, body-based cues alone (i.e. blind walking); Bv, body-based cues plus vision; D_1 , perception of the first travelled distance; D_2 , perception of the second travelled distance; D_p , perception of travelled distance based on combined input from the first and the second distance.

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Appendix

Here we explain in detail how the visual weights in Experiment 2 were calculated. To begin, we denote the reliabilities of the first and second visual and body-based estimates of walked distance, D_{1V} , D_{2V} , D_{1B} and D_{2B} , as $1/\sigma_{1V}^2$, $1/\sigma_{2V}^2$, $1/\sigma_{1B}^2$ and $1/\sigma_{2B}^2$, respectively. Here we show that w_{1V} and w_{2V} , the visual weights that contribute to D_1 and D_2 when vision is present in those conditions, can be calculated in two unique ways.

First, consider the B–B condition. Our model predicts $D_{P_BB} = (w_{1_BB}D_{1B} + (1 - w_{1_BB})D_{2B}) + a_{BB,i}$.

With reliability weighting we must have

$$w_{1_BB} = \frac{1/\sigma_{1B}^2}{1/\sigma_{1B}^2 + 1/\sigma_{2B}^2}. \tag{A1}$$

This allows the ratio, $\sigma_{1B}^2/\sigma_{2B}^2$, to be calculated from w_{1_BB} . Next, considering the Bv–B condition, we have

$$D_{P_BvB} = (w_{1_BvB}(w_{1V}D_{1V} + (1 - w_{1V})D_{1B}) + (1 - w_{1_BvB})D_{2B}) + a_{BvB,i},$$

and, therefore,

$$w_{1V} = \frac{1/\sigma_{1V}^2}{1/\sigma_{1V}^2 + 1/\sigma_{1B}^2}. \tag{A2}$$

The overall reliability of the D_1 component of the final estimate is given by $(\frac{\sigma_{1V}^2\sigma_{1B}^2}{\sigma_{1V}^2 + \sigma_{1B}^2})^{-1}$. Thus,

$$w_{1_BvB} = \frac{(\frac{\sigma_{1V}^2\sigma_{1B}^2}{\sigma_{1V}^2 + \sigma_{1B}^2})^{-1}}{(\frac{\sigma_{1V}^2\sigma_{1B}^2}{\sigma_{1V}^2 + \sigma_{1B}^2})^{-1} + \frac{1}{\sigma_{2B}^2}}. \tag{A3}$$

This result, along with Equation A1, allows w_{1_BB} and w_{1_BvB} to be used to calculate the ratio $\sigma_{1B}^2/\sigma_{1V}^2$. Putting this ratio into Equation A2 yields a value for w_{1V} . Thus, the B–B and Bv–B model equations were used to obtain a value of w_{1V} . Similarly, the combination of B–Bv and Bv–Bv model equations can be used to solve for w_{1V} as well. The value of w_{1V} reported in the main text was obtained by averaging these two estimates. Using the same methodology, an estimate w_{2V} was also found.