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RESEARCH ARTICLE

Contributions of visual and proprioceptive information to travelled distance estimation during changing sensory congruencies

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Abstract Recent research has provided evidence that visual and body-based cues (vestibular, proprioceptive and efference copy) are integrated using a weighted linear sum during walking and passive transport. However, little is known about the specific weighting of visual information when combined with proprioceptive inputs alone, in the absence of vestibular information about forward self-motion. Therefore, in this study, participants walked in place on a stationary treadmill while dynamic visual information was updated in real time via a head-mounted display. The task required participants to travel a predefined distance and subsequently match this distance by adjusting an egocentric, in-depth target using a game controller. Travelled distance information was provided either through visual cues alone, proprioceptive cues alone or both cues combined. In the combined cue condition, the relationship between the two cues was manipulated by either changing the visual gain across trials (0.7×, 1.0×, 1.4×; Exp. 1) or the proprioceptive gain across trials (0.7×, 1.0×, 1.4×; Exp. 2). Results demonstrated an overall higher weighting of proprioception over vision. These weights were scaled, however, as a function of which sensory input provided more stable information across trials. Specifically, when visual gain was constantly manipulated, proprioceptive weights were higher than when proprioceptive gain was constantly manipulated. These results therefore reveal interesting characteristics of cue-weighting within the context of unfolding spatio-temporal cue dynamics.

Keywords Optic flow · Proprioception · Multisensory integration · Distance estimation · Self-motion · Cue conflict

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Introduction

During everyday walking, dynamic visual information and information from the motor and vestibular systems are intrinsically linked. Understanding the interplay between these sensory signals is important for a wide variety of behaviours and applications. Studying tasks related to self-motion perception also provides a unique opportunity to better understand the mechanisms of multisensory integration during causally related interactions between internal (proprioceptive/vestibular/efference) and external (visual) sensory information.

A popular approach to quantifying relative cue-weighting has been to create a subtle conflict between the spatial or temporal characteristics of two or more sensory cues. In the context of self-motion perception, this has been done

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in the real world by, for instance, using glasses that alter visual inputs (e.g. prisms or magnifying/minifying goggles; Rushton et al. 1998; Campos et al. 2010), or more recently, by using virtual reality (VR) systems (e.g. locomotion while wearing head-tracked, head-mounted displays (HMD); Harris et al. 2000; Kearns et al. 2002, Kearns 2003; Sun et al. 2003, 2004; Proffitt et al. 2003; Durgin et al. 2005; Mohler et al. 2007a, b; Campos et al. 2012). By employing VR systems coupled with motion capture systems during walking, or coupled with motion simulators (e.g. wheelchairs, moving platforms) during passive movement, an observer's visual position and orientation in space can be tracked and updated in real time as a consequence of passive or active self-motion. Dissociations can be made by changing the relationship between the different sensory inputs so that there is no longer a consistent 1:1 relationship between two, typically coincident cues. This approach has been used in the context of estimating heading (Warren et al. 2001; Butler et al. 2010, 2011; Fetsch et al. 2010), speed (Banton et al. 2005), orientation (Klatzky et al. 1998; Kearns et al. 2002, Kearns 2003; Tcheang et al. 2011), distance travelled (Harris et al. 2000; Sun et al. 2004; Campos et al. 2010, 2012) and in describing the consequences of cue conflicts to biomechanical outputs (Prokop et al. 1997; Mohler et al. 2007a; Wright et al. 2013) (See Campos and Bülthoff 2011 for a review). For instance, Campos et al. (2012) used this approach to study cue-weighting during travelled distance perception. Participants estimated the length of a travelled distance while they were provided with either visual information alone (visual trajectory presented in an HMD), body-based information alone (proprioceptive + vestibular available during walked trajectories in the dark), both cues while combined and congruent (walking with updated vision), or both cues while combined, but incongruent. In the incongruent condition, a gain was placed on the visuals such that one unit of distance specified by body-based cues was associated with either 0.7× or 1.4× the visually travelled distances. By simultaneously presenting subjects with one distance visually and a different distance through body-based senses, this provided an opportunity to analyse the resultant distance estimates to see which sensory-specified distance the responses most closely approximated. The results indicated a higher weighting of body-based cues (proprioceptive + vestibular) compared to optic flow during full-scale walking (see also Campos et al. 2010 for complementary findings in the real world) and a roughly equal weighting of visual and vestibular inputs during passive travelled distance estimation (i.e. when being transported in a wheelchair).

Indeed, many of the studies that have set out to more specifically quantify relative cue-weighting during self-motion perception have also demonstrated a higher weighting of internal body-based cues over vision (Harris et al. 2000; Butler et al. 2010; Fetsch et al. 2010; Prsa et al. 2012). For instance, Butler et al. (2010) demonstrated a higher weighting of vestibular information compared to visual inputs during a passive heading perception task, and Harris et al. (2000) report a similar higher weighting of vestibular inputs when estimating passively experienced travelled distance trajectories. Others have systematically limited sensory information by, for instance, eliminating visual, vestibular or proprioceptive inputs to interpret effects on self-motion perception (Chance et al. 1998; Mittelstaedt and Mittelstaedt 2001; Jürgens and Becker 2006). However, by simply limiting individual cues, this does not provide direct insight into the relative weighting of each when both are available. To our knowledge, no studies have yet to explicitly describe the relative contributions of proprioceptive inputs and optic flow during walked distance estimation in the absence of vestibular cues signalling forward self-motion by using a sensory mismatch approach. Therefore, in Experiment 1 of the current study, we used a stationary treadmill set-up, combined with a HMD to specifically quantify the relative contributions of proprioceptive and visual cues during travelled distance estimation in the absence of vestibular inputs specifying forward motion. To do this, we manipulated the visual gains, thereby creating a subtle sensory conflict between optic flow and proprioceptive inputs. We then modelled the results using a Maximum Likelihood Estimation approach to determine whether the two modalities are combined using a weighted linear sum and to calculate the relative weights of vision and proprioception. Note also that, while it is certainly interesting to understand the general accuracy with which humans can estimate travelled distance, in this context, we are simply using travelled distance as a metric by which to gauge proportional differences in estimates across different sensory conditions.

One key feature of most past studies is that the method by which a conflict between visual and body-based cues is created is by placing the gain on the visuals, and thus, the visual speed/distance/direction associated with each unit of motoric/vestibular input is constantly changing across trials. It is therefore possible that a conflict created by manipulating the visual gains may change their relative reliability by altering their statistical correspondence with proprioceptive and vestibular inputs. Even if there is no conscious awareness of the constantly changing visual parameters, it is possible that through a process of adaptive responding across trials, the irregularities in the visual feedback may cause vision to be weighted less than the body-based cues (or weighted less than if they were constant across trials). Indeed, past research suggests that a flexible system of cue-weighting exists whereby statistical relationships are dynamically considered when assigning cue weights (Triesch et al. 2002; Baier et al. 2006). Therefore, in order to test whether relative cue-weighting is altered as a function of which individual sensory input is constantly changing, in Experiment 2, rather than manipulating visual gains during walking, we introduce motoric/proprioceptive gains by changing the speed of the treadmill across trials and keeping visual speed constant.

Experiment 1: Relative weighting of proprioceptive and visual cues

Methods

Participants

Sixteen participants (7 female) between the ages of 24–30 years completed all conditions. All participants had normal or corrected-to-normal visual acuity and were naïve to the purposes of the experiment. Participants were recruited through the Max Planck Institute Subject Database and were compensated at a rate of 8 Euros per hour. All participants provided informed written consent before beginning the experiment. This research was performed in accordance with the ethical standards specified by the 1964 Declaration of Helsinki.

Stimuli and apparatus

Participants walked on a large, linear treadmill (6.0 × 2.4 m; Bonte Technology, Zwolle, the Netherlands), the speed of which was controlled by a PC (baseline speed of 0.8 m/s). During the entire experiment, they grasped a bar in front of them that spanned the width of the treadmill. Head position and orientation were tracked using an optical tracking system (4 Vicon MX13 cameras) through the monitoring of helmet-mounted, reflective markers (See Fig. 1a). Each Vicon camera has a resolution of 1,280 × 1,024, and the sampling rate was 120 Hz. Tracked head information was used to update visual feedback from the virtual environments during head movements in real time.

Visual information about the virtual environment was presented via a HMD. The lightweight HMD used here (eMagin, Z800) has a resolution of 800 × 600 with a refresh rate of 60 Hz and a 40 degree diagonal FOV per eye. The HMD was embedded within a set of darkened goggles to ensure that none of the external laboratory environment was visible to participants at any time during the experiment. The VE was rendered using veLib, a customized VR communications and rendering library. The 3D model of the VE was developed using 3DMax and consisted of a seemingly infinite, empty hallway approximately 5 m wide and 3 m high. The walls and the floor of the hallway were mapped with a completely random texture with no repeating patterns or identifiable landmarks (See Fig. 1b). The target used for the response task consisted of an unfamiliar red and white striped sphere approximately 1 m in diameter. This target was always positioned in the centre of the hallway floor 2 m in front of the participant at the start of the response phase of each trial. Earplugs were used to reduce auditory cues, and headphones were used to present pink noise as a way of masking the sound of the treadmill. Subjects wore a safety harness during the entire study that ran along a cable above them without tension.

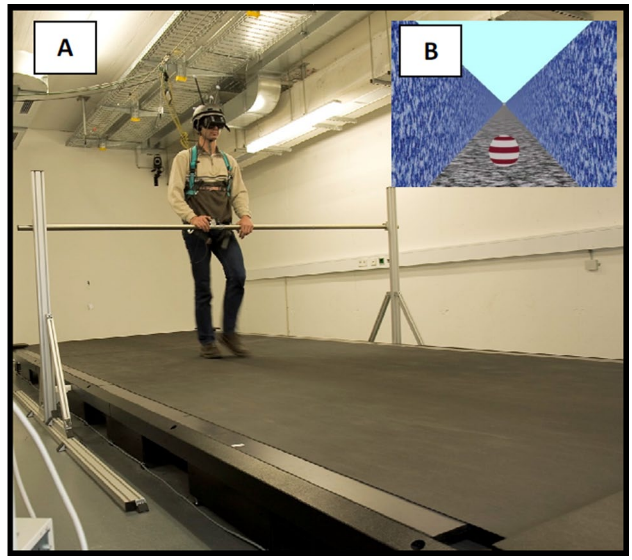

Fig. 1 Stimuli and apparatus. **a** Both experiments took place in a fully tracked space containing a large linear treadmill. Participants wore a helmet outfitted with reflective markers that were tracked using an optical tracking system (4 Vicon MX13 cameras). **b** The stimuli in both studies consisted of a seemingly infinite hallway with random texture on the walls and floor and the target consisted of a striped sphere

Procedure

In this task, participants were first required to travel down the hallway until reaching a predefined reference distance (4, 6, 8 or 10 m) which was unknown to the participant, at which point the screen went blank and the treadmill stopped. Subsequently, the target appeared in the hallway on the ground in front of them, and participants were asked to adjust the target using a game controller until the self-to-target distance matched the distance they had just walked. Once satisfied with the position of the target, responses were made via a button press. Each of the four distance intervals was repeated three times per condition in a pseudo-randomized order.

Baseline and practice

Each participant spent 5 min walking while wearing the HMD to become accustomed to moving within the VE. This also allowed for any necessary adaptation to occur to ensure a baseline perceptual-motor coupling. Within this time, participants also completed five practice trials without feedback to ensure that they were comfortable with the task.

Experimental conditions

Three conditions were conducted as a way of evaluating the relative contributions of optic flow and proprioceptive cues when estimating walked distances. In each of the experimental conditions, the response mode always remained the same (self-to-target distance reproduction). The sensory/motor information provided during the walked reference distance, however, varied as a function of condition. The order of conditions and the distance trials within conditions were pseudorandomized across and within participants, respectively.

Visual and proprioceptive cues combined

In the combined condition (*COM*), during the walked distance, the relation between optic flow and body-based cues was varied by manipulating the visual gain during forward movements. Three gain values of 0.7×, 1.0× (congruent) and 1.4× were used. By manipulating the visual gain, we were able to discretely provide participants with a visually specified travelled distance that was either longer or shorter than the motorically specified travelled distance (for a total of 12 visually specified distances). For instance, for a gain of 1.4×, if participants travelled a physical distance of 10 m, they would experience a motorically specified distance of 10 m, but a visually specified distance of 14 m. These gain values were determined in previous studies (Campos et al. 2012) to ensure that most participants were not consciously aware of the conflict and are within the range of gains that went undetected by participants in other studies (e.g. Steinicke et al. 2010). Across trials, the order of the gains was randomized in such a way that adaptation effects would be highly unlikely. Each of the four distances was repeated three times for each of the three gain levels resulting in 36 trials in total.

Vision alone

In the vision alone condition (*VIS*), participants stood stationary while viewing a visual trajectory of the movement down the hallway. Information from the x-, y- and z-dimensions (i.e. forward head motion, head bob, lateral sway, respectively) was continuously tracked and updated online as the participant viewed the translational movement. In other words, if participants looked around during the visually simulated travelled distance, these head movements would be updated appropriately in the display. Three visual speeds were included in the *VIS* condition and were used to represent travelled distances that were equivalent to the visual distances resulting from the three gains introduced in the *COM* condition (i.e. 0.7×, 1.0× and 1.4× of 4, 6, 8 and 10 m; for a total of 12 distances) so that these values could be entered into the model to make predictions.

Proprioceptive cues alone

In the proprioceptive cue alone (*PROP*) condition, participants walked the distances in the complete absence of visual inputs. In this case, the HMD presented a blank screen during walking other than the prompts to commence and terminate the walked distance prior to responding. The hallway and target appeared again once it was time to make their self-to-target estimate.

Leaky integrator

The presented distance travelled for the visual, proprioceptive and congruent combined conditions was each fitted by a leaky spatial integrator model for Experiments 1 and 2 (Lappe et al. 2007; Harris et al. 2012). The model describes the change of presented distance travelled (p) with respect to the change of the adjusted target distance estimate (x).

$$\frac{\mathrm{d}p}{\mathrm{d}x} = -\alpha p + k \tag{1}$$

where k and α are the sensory gain and the leak rate, respectively; when $k = 1$ and $\alpha = 0$, the formula describes the ideal observer such that the perceived distance is equal to the presented distance $p = x$. The general solution of the leaky spatial integrator is

$$p = \left(\frac{k}{\alpha}\right)(1 - \exp(-\alpha x)) \tag{2}$$

Rearranging the equation, we have

$$x = \left(-\frac{1}{\alpha}\ln\left(1 - \left(\frac{\alpha}{k}\right)p\right)\right) \tag{3}$$

Due to distances being scaled differently in VR (see Loomis and Knapp 2003; Thompson et al. 2004), each participant's average-adjusted target distance for the four distances (4, 6, 8 and 10 m) was normalized within condition with respect to the average response for the shortest target distance (4 m), for example (Normalized Visual Response) = (Visual Response)/(Visual Response to 4 m). Similarly, the presented distance was normalized with respect to the shortest distance (4 m), resulting in the ratios 1, 1.5, 2 and 2.5.

$$\text{Normalized Response Distance} = \left(\frac{\text{Response Distance}}{\text{Response Distance to 4m}}\right) \tag{4}$$

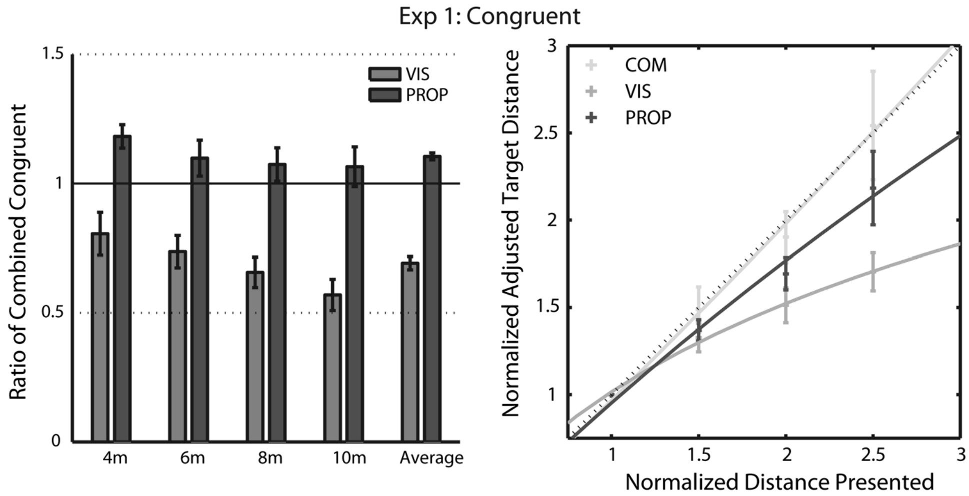

Fig. 2 Comparing across sensory conditions in Experiment 1. **a** *Left* Experiment 1 results. Illustrating the average *distance ratio* scores between the two unisensory conditions (*VIS* and *PROP*) and the combined and congruent condition (COM at ×1.0 represented by the *solid horizontal line*). Averaged data are shown for each distance and also collapsed across distances. *Error bars* represent standard errors. **b** *Right* Normalized adjusted distance versus normalized presented distance for the *VIS*, *PROP* and *COM* conditions. The plus sign and *error bars* are the average and standard errors. The *dashed line* indicates the ideal observer. The *continuous lines* are the fit by the leaky integration model

$$\text{Normalized Presented Distance} = \left(\frac{\text{Presented Distance}}{4}\right) \tag{5}$$

The leaky spatial integrator model was fit using a least squares algorithm which resulted in two parameters and one fit parameter per condition for each participant; the sensory gain (k), the leak rate (α) and the squared correlation coefficient (r^2) of the fit.

Results

Multisensory versus unisensory conditions

Of main interest to the current study was the relative difference in estimates across the three different conditions rather than the accuracy of absolute distance estimates per se. Therefore, for each participant, we calculated the distance ratio between their average estimates for each distance in the *COM* and congruent (1.0×) condition and their average estimates for each distance in each of the *VIS* and *PROP* conditions (i.e. *VIS/COM (1.0×)* and *PROP/COM (1.0×)*). These values were then averaged across participants (See Fig. 2).

Results demonstrated that travelled distance estimates for the *PROP* condition (M for each distance, 4, 6, 8, 10 m = 7.34, 10.05, 12.42, 16.02) were on average 10 % longer than the combined and congruent condition (M = 6.12, 9.11, 11.65, 15.57), while distance estimates for the *VIS* condition (M = 4.65, 6.18, 7.04, 7.93) were 31 % shorter than the combined and congruent condition (See Fig. 2a). A three (Condition: *VIS/COM, COM/COM, PROP/COM*) × four (Distance: 4, 6, 8, 10 m) repeated-measures ANOVA was conducted on distance ratio scores and demonstrated a main effect of condition [F (2, 14) = 17.95, $p < 0.001$], a main effect of distance [F (3, 13) = 4.40, $p < 0.05$] and an interaction effect [F (6, 10) = 3.31, $p < 0.05$]. Planned comparisons demonstrated significant differences between the *COM* (1.0×) and *VIS* conditions [F (1, 15) = 27.55, $p < 0.001$] and the *COM* (1.0×) and *PROP* conditions approached significance [F (1, 15) = 3.88, $p = 0.06$].

Leaky integrator model

The normalized results for all three conditions were fit to a leaky spatial integrator (Fig. 2b); the participant mean and standard error of the squared correlation coefficient (r^2) of the fit for the three conditions were *VIS* (0.77 ± 0.06), *COM* (0.90 ± 0.03) and *PROP* (0.94 ± 0.02). It should be noted that while the mean squared correlation coefficients were very high, the VIS condition was significantly lower than both the COM and PROP conditions. To investigate the relationship of sensory gain and sensory modality, a one-way repeated-measures ANOVA with the three levels (Condition: VIS, COM, PROP) was conducted and demonstrated a main effect of condition [F (2, 45) = 6.25, $p < 0.005$]. Planned comparisons demonstrated significant differences between the COM and VIS conditions ($t_{\text{df}=15}$ = 3.7,

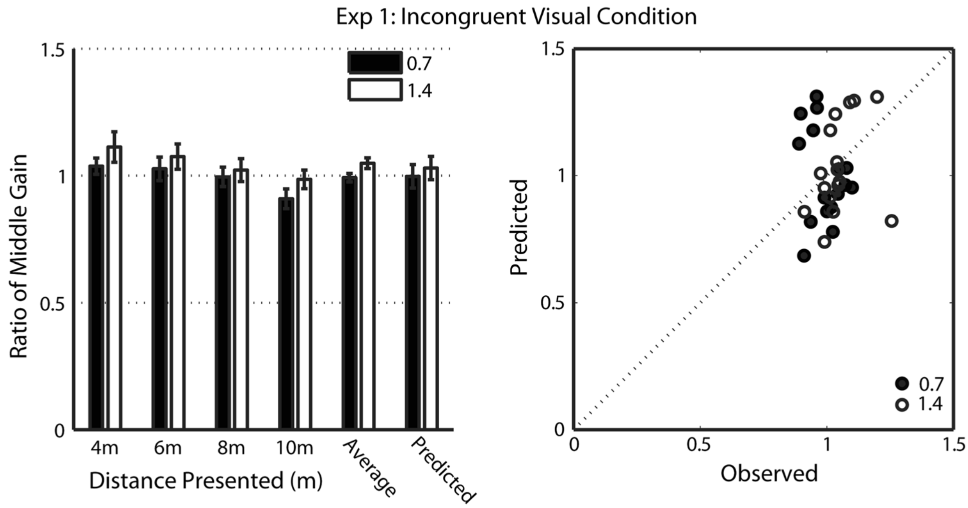

Fig. 3 Effects of visual gain changes in Experiment 1: **a**. *Left* Experiment 1 results illustrating the average *distance ratio* scores between the low gain trials (×0.7) versus the congruent trials (×1.0) and between the high gain trials (×1.4) and the congruent trials (×1.0) when visual gain was varied. Averaged data are shown for each distance and collapsed across distances. Predictions based on MLE are also plotted. *Error bars* represent standard errors. **b** *Right* Scatterplot of observed distance estimates versus predicted distance estimates. *Filled* and *open circles* represent different gain factors for each participant. The *dashed line* indicates the ideal data

$p < 0.005$) and the PROP and VIS condition ($t_{df=15} = 3.83$, $p < 0.005$). To investigate the relationship between the leak rate and sensory modality, a one-way repeated-measures ANOVA with the three levels (Condition: VIS, COM, PROP) was conducted and demonstrated a main effect of condition [F (2, 45) = 3.684, $p < 0.05$]. Planned comparisons demonstrated significant differences between the *COM* and *VIS* conditions ($t_{df=15} = 2.33$, $p < 0.05$) and the *PROP* and *VIS* condition ($t_{df=15} = 2.24$, $p < 0.05$). These results indicate a stronger effect of distance on the response in the *VIS* condition compared to the *PROP* and *COM* conditions.

Effect of changing visual gain

In the *COM* condition, distance estimates in the high visual gain trials (1.4×) (M = 6.68, 9.65, 11.80, 15.54) were on average 5 % longer than in the congruent trials (1.0×) (M = 6.12, 9.11, 11.65, 15.57), while distance estimates in the low visual gain trials (0.7×) (M = 6.28, 9.11, 11.50, 14.15) were 1 % shorter than the congruent trials (See Fig. 3a). A three (Gain; 1.4×/1.0×, 1.0×/1.0× and 0.7×/1.0×) × four (distance) repeated-measures ANOVA conducted on distance ratio scores demonstrated no significant effect of Gain, no main effect of Distance and no interaction effects.

Model predictions assuming a linearly weighted summation

If the unimodal cues (*VIS*, *PROP*) are integrated using a weighted average, then the combined and congruent condition (COM at 1.0×) can be expressed as a linear sum

$$\mathrm{COM} = w_{\mathrm{VIS}}\mathrm{VIS} + w_{\mathrm{PROP}}\mathrm{PROP} \quad w_{\mathrm{VIS}} + w_{\mathrm{PROP}} = 1 \tag{6}$$

where w_{VIS}, w_{PROP} are the weights for the unimodal visual and body conditions. As participants only performed three repetitions per distance, the mean data for each distance were used to calculate the groups' weights.

For the unimodal and congruent conditions, the observed visual and body weights were calculated from

$$w_{\mathrm{VIS}} = \frac{\mathrm{COM} - \mathrm{PROP}}{\mathrm{VIS} - \mathrm{PROP}} \quad w_{\mathrm{PROP}} = \frac{\mathrm{COM} - \mathrm{VIS}}{\mathrm{PROP} - \mathrm{VIS}} = 1 - w_{\mathrm{VIS}} \tag{7}$$

The observed weights indicate the extent to which each modality was relied upon during walking. The closer each modality's weight is to 1.0, the more it was relied upon in the combined and congruent condition. The observed group average weights are $w_{\mathrm{VIS}} = 0.22$ and $w_{\mathrm{PROP}} = 0.78$, thus suggesting a higher reliance upon body-based cues. Interestingly, visual weight seemed to be systematically related to distance, with lower weights associated with longer distances: 4 m (w_{VIS} 0.45), 6 m (w_{VIS} 0.24), 8 m (w_{VIS} 0.14) and 10 m (w_{VIS} 0.06).

The unimodal observed weights were then used to make predictions for the incongruent conditions using

$$\mathrm{Pred}^{\mathrm{Gain}} = w_{\mathrm{VIS}}\mathrm{VIS}^{\mathrm{Gain}} + (1 - w_{\mathrm{VIS}})\mathrm{PROP}. \tag{8}$$

where $\mathrm{Pred}^{\mathrm{Gain}}$ is the predicted distance estimate of the combination of the visual and body-based cue estimates for each of a given distance and a given gain factor. Thus, 12 predictions were calculated for each participant, one for each of the four distances at each of the three gain levels. To test whether these predictions are consistent with the observed data in the incongruent conditions, a two (Observed vs. Predicted) × three (Gain: 0.7×, 1.0×, 1.4×) × four (Distance: 4, 6, 8, 10 m) repeated-measures ANOVA was conducted on the *distance ratio* scores. The results demonstrated no significant difference between Observed and Predicted values [F (1, 15) = 0.00, $p > 0.05$], a significant main effect of gain [F (2, 14) = 4.54, $p < 0.05$] and no significant main effect of distance [F (3, 13) = 2.08, $p > 0.05$] (See Fig. 3b).

To investigate the prediction accuracy of the linear model, the observed and predicted data were submitted to a linear regression analysis with the intercept set to 0. The choice of setting the intercept to 0 enabled a more direct comparison with the ideal model (predicted = β observed, where $\beta = 1$). The results showed a significant relationship between the observed and predicted data, $\beta = 0.98867 \pm 0.03303$, t (31) = 29.93, $p < 0.001$. The observed data explained a significant proportion of variance in the predicted weighted sum, $R^2 = 0.97$, F (1, 31) = 895.84, $p < 0.001$. Furthermore, the ideal model beta weight ($\beta = 1$) lies within the range of the observed beta weights (0.956, 1.02).

Experiment 2

In Experiment 2, we assessed whether the sensory system upon which the gain is placed (and thus the sensory system with more constantly changing parameters) affects the relative weighting of the individual cues. We tested this by placing the gain on the proprioceptive inputs while keeping the visual speed constant across trials.

Methods

Participants

Twenty participants (6 female) between the ages of 21–34 years completed all conditions. All participants had normal or corrected-to-normal visual acuity and were naïve to the purposes of the experiment. They were recruited through the Max Planck Institute Subject Database and were compensated at a rate of 8 Euros per hour.

Ethics statement

All participants provided informed written consent before beginning the experiment. This research was performed in accordance with the ethical standards specified by the 1964 Declaration of Helsinki. Because it involved standard testing procedures for research in non-public institutions and did not involve drugs, it did not require any additional ethics approval from the ethics review board.

Stimuli and apparatus

The laboratory, treadmill and visualization set-up (Virtual Environment and the HMD) were identical to that used in Experiment 1

Procedure

The same four conditions were used in Experiment 2 as were used in Experiment 1, with the exception that the gain was placed on the motorically specified distance by changing the treadmill speed. These conditions were therefore *COM*, *VIS* and *PROP*. The same four distances (4, 6, 8, 10 m) were repeated four times per condition and four times for each gain (or distance equivalent to each gain) in the *COM* condition and *PROP* conditions (gains of 0.7×, 1.0, 1.4).

Results

Multisensory versus unisensory conditions

Distance estimates for the *PROP* condition (M = 10.41, 13.85, 16.54, 18.77) were on average 22 % longer than the *COM* congruent condition (M = 8.89, 12.10, 14.29, 15.85), while distance estimates for the *VIS* condition (M = 6.55, 7.58, 9.33, 10.88) were 27 % shorter than the *COM* congruent condition (See Fig. 4a). A three (Condition: *PROP/COM, COM/COM, VIS/COM*) × four (Distance: 4, 6, 8, 10 m) repeated-measures ANOVA was conducted on distance ratio scores and demonstrated a main effect of Condition [F (2, 18) = 23.49, $p < 0.001$], no main effect of Distance and no interaction effect. Planned comparisons demonstrated significant differences between the *COM* and *VIS* conditions [F (1, 19) = 13.41, $p < 0.01$] and the *COM* and *PROP* conditions [F (1, 19) = 16.56, $p = 0.01$].

Leaky integrator model

The normalized results for all three conditions were fit to a leaky spatial integrator model (Fig. 4b); the participant mean and standard error of the squared correlation coefficient (r^2) of the fit were VIS (0.79 ± 0.05), COM (0.86 ± 0.04) and PROP (0.87 ± 0.03). To investigate the relationship between sensory modality and gain factor, a one-way repeated-measures ANOVA with the three levels (Condition: VIS, COM, PROP) was conducted and demonstrated no main effect of Condition [F (2, 60) = 0.35,

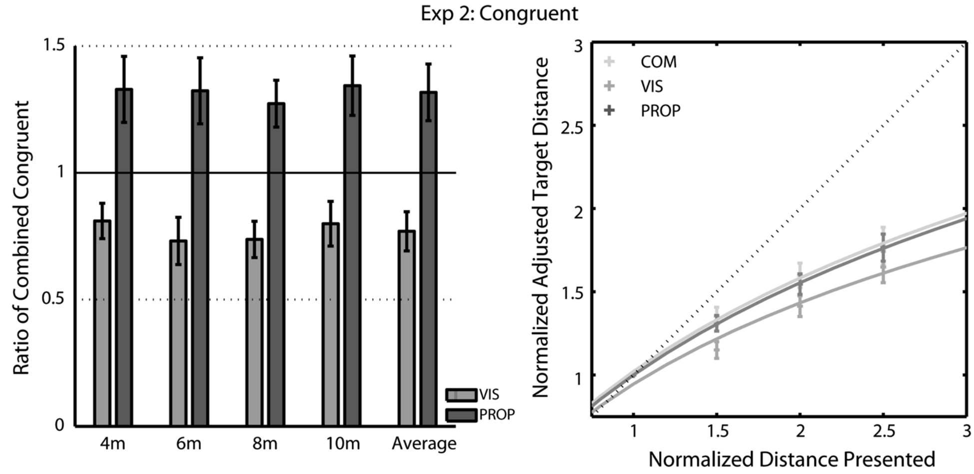

Fig. 4 Comparing across sensory conditions in experiment 2: **a** *Left* Experiment 2 results illustrating the average *distance ratio* scores between the two unisensory conditions (*VIS* and *PROP*) and the combined and congruent condition (COM at ×1.0 represented by the *solid horizontal line*). Averaged data are shown for each distance and also collapsed across distances. *Error bars* represent standard errors. **b** *Right* normalized adjusted distance versus normalized presented distance for the *VIS*, *PROP* and *COM* conditions. The *plus sign* and *error bars* are the average and standard errors. The *dashed line* indicates the ideal observer. The *continuous lines* are the fit by the leaky integration model

$p = 0.71$]. To investigate sensory modality and the leak rate, a one-way repeated-measures ANOVA with the three levels (Condition: VIS, COM, PROP) was conducted and demonstrated no main effect of Condition [F (2, 60) = 0.21, $p = 0.81$).

Effect of changing proprioception gain

In the *COM* condition, the average distance estimates across all 12 participants in the high visual gain trials (1.4×) (M = 11.91, 15.05, 18.24, 20.82) were 35 % longer than in the congruent trials (1.0×), (M = 8.89, 12.10, 14.29, 15.85), while distance estimates in the low visual gain trials (0.7×) (M = 7.34, 10.46, 12.46, 13.38), were 13 % shorter than the congruent trials (See Fig. 5a). A three (Gain; 0.7×/1.0×, 1.0×/1.0×, 1.4×/1.0×) × four (Distance) repeated-measures ANOVA on *distance ratio* scores demonstrated a significant main effect of Gain [F (2, 18) = 22.13, $p < 0.001$], no main effect of Distance and no interaction effect. Planned comparisons demonstrated significant differences between the high gain trials compared to congruent trials [F (1, 19) = 33.84, $p < 0.001$] and the low gain trials compared to congruent trials [F (1, 19) = 38.79, $p < 0.001$].

Model predictions assuming a linearly weighted summation

Using the unisensory and combined congruent data, the weights were calculated to be, on average, $w_{\mathrm{VIS}} = 0.40$ and $w_{\mathrm{PROP}} = 0.60$, thus suggesting a higher reliance upon body-based cues. In this case, the weights did not appear to change systematically as a function of distance, with calculated visual weights for 4, 6, 8, 10 m trials of 0.48, 0.34, 0.36 and 0.43, respectively.

The unimodal observed weights were then used to make predictions for the incongruent conditions using the same method as described in Experiment 1. To test whether these predictions are consistent with the observed data in the incongruent conditions, a two (Observed vs. Predicted) × three (Gain: 0.7×, 1.0×, 1.4×) × four (Distance: 4, 6, 8, 10 m) repeated-measures ANOVA was conducted on the *distance ratio* scores. The results demonstrated no significant difference between Observed and Predicted values [F (1, 19) = 0.009, $p > 0.05$], a significant main effect of gain [F (2, 18) = 44.26, $p < 0.001$] and no significant main effect of distance [F (3, 17) = 1.13, $p > 0.05$] (See Fig. 5b).

Similar to Experiment 1, to test the prediction accuracy of the model, the observed and predicted data were submitted to a linear regression analysis with the intercept set to 0. The results showed a significant relationship between the observed and predicted data, $\beta = 1.056 \pm 0.057$, t (41) = 18.37, $p < 0.001$. The observed data explained a significant proportion of variance in the predicted weighted sum, $R^2 = 0.89$, F (1, 41) = 337.28, $p < 0.001$. Furthermore, the ideal model beta weight ($\beta = 1$) lies within the range of the observed beta weights (0.999, 1.113).

Comparison of visual weights in Experiment 1 and Experiment 2

To investigate cue stability, the visual weights from Experiment 1 and Experiment 2 were compared for the 4

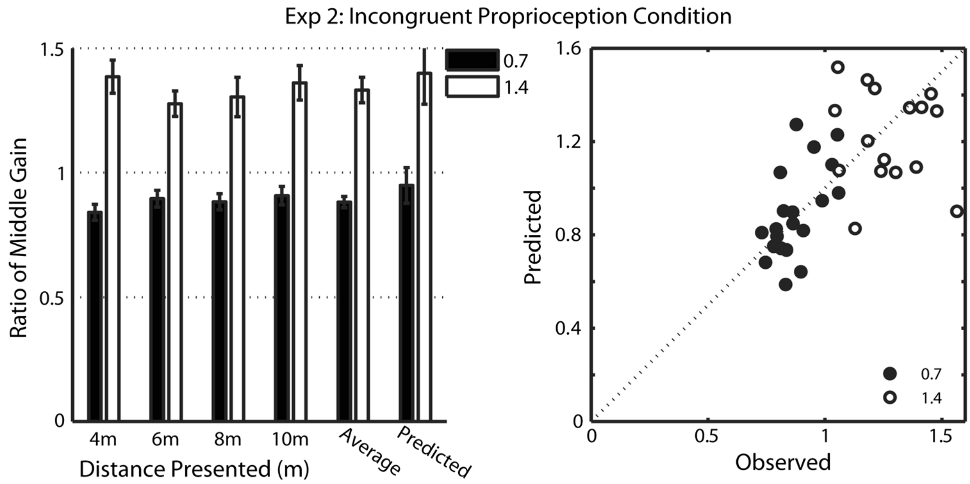

Fig. 5 Effects of proprioceptive gain changes in experiment 2: **a** *Left* experiment 2 results illustrating the average *distance ratio* scores between the low gain trials (0.7×) versus the congruent trials (1.0×) and between the high gain trials (1.4×) and the congruent trials (1.0×) when proprioceptive gain was varied. Averaged data are shown for each distance and collapsed across distances. Predictions based on MLE are also plotted. *Error bars* represent standard errors. **b** *Right* Scatterplot of observed distance estimates versus predicted distance estimates. *Filled* and *open circles* represent different gain factors for each participant. The *dashed line* indicates the ideal data

distances (4, 6, 8 and 10 m). Due to the small sample size ($N = 4$), a nonparametric Monte Carlo bootstrap analysis was employed to paint the distribution of the differences of the visual weights. For a single bootstrap statistic, the data from each experiment was resampled with replacement and average, and the bootstrapped averages from Experiment 1 and Experiment 2 were subtracted. This procedure was run 1,000 times to describe the distribution. The null hypothesis is that the distribution is centred on 0, which would imply there are no differences between the weights in Experiment 1 and Experiment 2. The results show that the 0 mean does not lie within the 95 % bootstrapped confidence intervals of the distribution of the differences of visual weights hence rejecting the null hypothesis. This result suggests that the weights are different for the two experiments implying that the stability of the weights is affected by the experimental manipulation.

General discussion

Overall, the results of these two studies demonstrate a consistent combined effect of visual and proprioceptive cues when both are available during walking in place. This was evidenced by the fact that distance estimates for combined cue trials always fell somewhere between the estimates for each of the unisensory trials. This indicates that neither cue was used exclusively in generating an estimate of travelled distance. However, when calculating relative weights, there was a significantly greater weight assigned to proprioceptive cues. This higher weighting of proprioception was observed irrespective of whether the visual-motor relationship was changed as a function of constantly altered visual or constantly altered proprioceptive inputs. However, the source of the gain change (visual or proprioceptive) did, in fact, affect relative cue-weighting across the two experiments. Specifically, when visual gain was manipulated across trials, proprioceptive weights were higher compared to when proprioceptive gain was manipulated across trials, in which case proprioceptive weights were lower. This suggests that the mode by which cue relations are changed within recent history appears to dynamically affect relative cue-weighting.

Higher weighting of proprioceptive inputs over optic flow while walking in place

The higher reliance on proprioceptive inputs while walking in place is supported by other research indicating that, even in the absence of vestibular inputs about forward self-motion, information from the legs via commanded (i.e. efference copy) and sensed (i.e. proprioceptive) information can be highly informative in tasks requiring self-motion perception and spatial updating. Information from the legs, which integrates information about step length, step rate and load, has been shown to be a consistent metric by which humans (Durgin et al. 2009) and other terrestrial animals, such as ants (Wittlinger et al. 2006; Steck et al. 2009), rely upon in the absence of vision. For instance, Mittelstaedt and Mittelstaedt (2001) have shown that participants can accurately estimate the length of a travelled path when walking in place on a conveyor belt in the absence of vision and have argued that proprioception/efference copy is particularly important for accurate path integration. Glasauer et al. (1994, 2002) have also shown that labyrinthine-defective subjects can still estimate walked distance while blindfolded, indicating that even in the absence of reliable vestibular inputs, self-motion can be effectively estimated. Neurophysiological evidence showing the importance of leg movements to spatial representations has been recently provided by a VR study in mice. Specifically, Chen et al. (2013) demonstrated that during simulated motion down a linear path, proprioceptive/efferent copy information provided by running in place on a rotating ball strongly affected the firing of place cells compared to conditions of pure visual motion. Finally, while Sun et al. (2004) demonstrated a nonlinear weighting of visual and proprioceptive information during travelled distance estimation while riding a stationary bicycle, visual information was shown to be weighted higher in that study. This poses the interesting question of how different types of proprioceptive inputs affect cue-weighting across different tasks. In particular, for travelled distance estimation, step length information, for instance, becomes a consistent and reliable metric that is correlated with the extent of visual motion. Pedal rotations on a bicycle, however, are not as tightly coupled with extent of visual motion in the absence of extensive experience or in the event of gear changes.

We have recently argued that, unlike other forms of sensory integration between exteroceptive cues (i.e. auditory-visual integration) where large multisensory conflicts lead to a breakdown in integration, in the context of natural, overground walking, mandatory integration may take place between vestibular and proprioceptive cues given their very strong coupling (Frissen et al. 2011, 2013). As evidence of this, we describe a phenomenon whereby the perception of illusory forward self-motion is experienced while an observer is walking in place (i.e. "vection from walking" see also Bles and Kapteyn 1977; Bles 1981). Specifically, we argue that, while walking in place, a nonzero proprioceptive input mandatorily combines with a conflicting zero vestibular input, thus invoking a perception of forward motion. These results support the notion that when walking in place on a treadmill, as was the case in the current study, a sense of forward self-motion may persist, even in the absence of physical forward motion.

Finally, it is important to note that it is not clear how well proprioceptive/efferent copy inputs during walking in place can support more complex transformations (e.g. Frissen et al. 2011) or support distance estimation over much larger distances (Souman et al. 2009; Frissen et al. 2013). The approach used in the current study also does not allow us to comment on how accurate the perception of travelled distance is across the different sensory conditions. Because distances are typically compressed in VR (Loomis and Knapp 2003; Thompson et al. 2004), it is not reasonable to assess how close to veridical distance perception is in this context. VR does, however, provide a unique opportunity to carefully manipulate the availability of different sensory inputs, and therefore, the results speak clearly to the *relative* contributions of sensory/motor inputs during walking in place.

Changing cue relations via different sensory modalities and the effect on relative cue-weighting

Even though proprioceptive cues were weighted higher in both Experiments 1 and 2 irrespective of how the incongruency was introduced, the modality upon which the gain was manipulated did affect the value of the weights. Specifically, the weight of proprioception was reduced when the motorically specified distance (for each unit of visual distance) was changed constantly across trials (Exp. 2) compared to when visually specified distances were changed constantly across trials (Exp. 1). It is important to note that the absolute reliability of each cue on any given trial did not change and the degree of conflict between the two never changed. Unlike findings that describe how the degree of spatial or temporal conflict affects relative cue weights (Gepshtein et al. 2005), these results speak to the role that the recent history of cue relations can play in determining relative cue-weighting.

In the context of visual cue integration, Triesch et al. (2002) asked participants to perform a visual tracking task while the consistency of the tracked object characteristics (colour, shape and size) changed dynamically within each trial. They then evaluated the extent to which each visual cue was relied upon to perform the task. For trials in which a particular visual cue changed repeatedly, this cue was weighted less than cues that remained constant throughout the trial. Essentially, higher weights were assigned to cues that were more stable within the recent past, whereas lower weights were assigned to cues that frequently changed. These changes to cue integration appeared to happen adaptively and very quickly (i.e. within 1 s.). In a sense, the current results support a somewhat analogous multisensory example of this phenomenon whereby the stability of the spatio-temporal characteristics of a sensory cue specifying self-motion may affect the extent to which it is weighted in the final estimate. While a time course analysis is not possible here due to a limited number of trials, future research could help to describe the dynamics of changing cue weights as a function of continuously changing cue relations. It would also be very interesting to evaluate the time course of sensory weighting in the context of adaptation paradigms that introduce prolonged sensory conflicts, unlike the transient and constantly changing (in direction and magnitude) cue conflicts introduced here.

The results of the Leaky Spatial Integrator fit in Experiment 1 show a larger gain factor and a faster leak rate for the visual cues than the proprioceptive and the combined cues, thus suggesting that over longer distances, the visual cues deviate more from the ideal observer. This, in combination with the introduction of visual gain changes in Experiment 1, could contribute to a reduction of visual weights as a function of distance. In contrast, in Experiment 2, the fits of the Leaky Spatial Integrator for the three conditions resulted in comparable leak rates and gain factors. This could be due to the introduction of proprioceptive gain changes, which do not seem to as strongly affect distance estimates within the range of distances presented here.

It is often argued in the extensive multisensory literature that experimentally created cue conflicts are a valid approach to quantifying cue-weighting in a way that reflects normal behavioural conditions (e.g. De Gelder and Bertelson 2003; Fetsch et al. 2013). In support of this, it is typically reasoned that indeed, individual modalities can provide conflicting information even under naturally occurring circumstances. In the case of walking, for instance, there are situations where movement from the legs is associated with altered amounts of visual motion, such as when walking on a moving sidewalk or when walking through a train. The brain can typically resolve these discrepancies with ease. However, that is not to say that the relative cue-weighting under these circumstances reflects the same cue weights as would be observed in the absence of these atypical or modified cue relations (particularly for extended or frequently changed cue relations). Nonetheless, the cue conflict approach to quantifying relative cue-weighting remains a very important tool in modelling underlying multisensory processes by providing a way in which to dissociate individual sensory estimates. However, the method by which the conflict is introduced (and via which sensory system) should be carefully considered when interpreting the results.

Finally, it is not clear how the biomechanics of walking changed during treadmill walking in both the combined and proprioception alone conditions. It is known that for natural walking within the range of speeds tested here, stable walking parameters such as the walk ratio (i.e. step rate divided by step length) do not change (Multon and Olivier 2013). Therefore, it is not expected that the changing speeds that were coincident with different proprioceptive gains introduced in Experiment 2 are what lead to a reduction in proprioceptive weights. It is also possible that the introduction of visual gain changes in Experiment 1 may also have biomechanical consequences (Prokop et al. 1997; Mohler et al. 2007a); however, it would be expected that any biomechanical instabilities introduced via visual manipulations would reduce proprioceptive weights rather than increase them (as was observed here). Further, it is also important to consider that the proprioceptive information generated when walking on a treadmill (and the treatment of this information during cue-weighting) may be different compared to walking over firm ground (Van Caekenberghe et al. 2013). Yet, again, any such differences, while possibly having an overall scaling effect, would not be predicted to result in a lower weighting of proprioceptive information within this context. In general, a better description of the biomechanical features of walking in place under difference sensory conditions would provide additional insight into the interplay between visual and proprioceptive interactions (e.g. through use of kinematic data collected using motion tracking). Another possible approach to gain a deeper understanding of the different contributions of visual and proprioceptive cues during walking could be to use recent advances in neuroimaging techniques which have made it feasible to acquire electrophysiological responses during self-motion (Nolan et al. 2009, 2012, Gwin et al. 2011, De Sanctis et al. 2012). This would help to isolate the different processes and time courses of different sensory estimates across space and time.

Overall, this study supports previous findings that indicate a dominant role for body-based cues over dynamic visual flow in the estimation of travelled distances. The current results support the contention that proprioceptive/efference copy information continues to contribute significantly to spatial processing in the absence of vestibular inputs to forward self-motion. Importantly, proprioceptive weights in this case were scaled as a function of the consistency of individual cues across recent trial history, such that higher proprioceptive weights were observed when motoric speed remained stable across trials and lower proprioceptive weights were observed when motoric speed constantly changed. These results, therefore, emphasize the need to better understand the principles underlying multisensory integration within the context of unfolding cue dynamics.

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