**Neither the richness of optic flow, nor the precision of heading judgements,
predicts walking trajectories.**

Danlu Cen, Simon K. Rushton*, Seralynne D. Vann
*School of Psychology, Cardiff University,
Tower Building, Park Place, Cardiff, CF10 3AT, UK*

*** Corresponding author:** *Simon Rushton*
School of Psychology
Cardiff University
Park Place
Cardiff, CF10 3AT
Wales, UK

rushtonsk@cardiff.ac.uk
+44 29 208 70086

Abstract

When an observer translates through space, a pattern of image motion, “optic flow”, is projected onto the back of each eye. If the translation is forwards, a radial pattern of optic flow results, with the center of the pattern specifying the direction of translation. It is commonly assumed that humans use optic flow in the visual guidance of walking and that the contribution of optic flow is proportional to its richness. A further assumption is that “heading” judgements (judgements of the direction of translation) and guidance of walking rely on the same visual information and thus the processes involved in the latter can be studied using the former. These assumptions underpin a very extensive body of psychophysical, behavioral, neurophysiological, clinical, computational modelling and imaging research. We measure the form of walking trajectories (using a standard perturbation design in Experiment 1) and the precision of heading judgements (Experiment 2) in four different visual environments. We find that neither the richness of optic flow nor the precision of heading judgements predicts walking trajectories. These results challenge the widely held assumptions about optic flow, perception of heading and the visual guidance of walking.

Keywords:

Optic flow, Visual guidance of locomotion, perception and action, allocentric cues, perceptuo-motor control

Introduction

Forward translation of the observer through space produces a radial pattern of optical motion (“optic flow”, a field of velocity vectors) at the eye. When walking to a visible target the observer uses the information available in the flow field (the most salient feature is the center of the radial flow pattern, the “focus of expansion” or FoE, which indicates the current direction of translation) to guide walking. The sensitivity of the human brain to the information that is used in the guidance of walking can be measured by presenting observers with optic flow and measuring the precision of judgements of translation direction – “heading”. The neural processing underpinning the guidance of walking can be investigated using brain imaging or electrophysiology with optic flow displays. Computational models that describe and predict walking behavior can be built on data from psychophysical heading judgements. The assumptions listed above underpin an extensive body of work in psychophysics (e.g., Lappe, Bremmer, & Van Den Berg, 1999; Warren, Mestre, Blackwell, & Morris, 1991; Warren, Morris, & Kalish, 1988), imaging (e.g., Cardin & Smith, 2011; Greenlee, 2000; Sherrill et al., 2015) and modelling (e.g., Lappe, 1998, 2000; Perrone & Stone, 1994; Royden, 1994; Warren & Fajen, 2004). The data we present here challenges these assumptions*.

Richness of optic flow and the guidance of walking

We start with a brief overview of a key study (Warren, Kay, Zosh, Duchon, & Sahuc, 2001) that provides a motivation and template for the experiments reported here. In the study, participants walked towards a target in a virtual environment. Use of a virtual reality technology allowed the investigators to create a situation that is seldom encountered under normal circumstances. Based on the standard techniques (Rushton, Harris, Lloyd, & Wann, 1998) to investigate cue use, the authors introduced an offset between visual direction and movement direction such that a step physically straight ahead would produce a step in the virtual environment that was 10° away from straight ahead. If the observer walked to keep the focus of expansion (FoE) aligned with the target (*optic flow* strategy), the observer would take a straight path to the target[†] (see Figure 1b). If the observer walked to keep the target visually straight ahead (the *egocentric direction* strategy, Rushton, Harris, Lloyd, & Wann, 1998), the observer would take a curved (10° equi-angular spiral) path to the target (see

* Data have been published previously in abstract form (Cen, Rushton, & Vann, 2015).

[†] After an initial step in the direction of the target before optic flow was available.

Figure 1a). By measuring the degree of curvature of the resultant trajectories, the relative contribution of the two cues (optic flow and egocentric direction) to the visual guidance of walking could be quantified; the straighter the trajectories, the greater the use of optic flow (see Figure 1c).

Figure 1. Schematic illustration of the strategy used by an observer relying solely on optic flow (a) or the egocentric direction of the target (b). Dark blue bar represents the target, and light blue bar the image of the target seen through the prism. The prism shifts the whole image of the scene including the target to the right by 10° . When the observer takes a step in the visual direction of the target, he/she moves in a slightly offset (10°) direction in the environment. (a) **Optic flow strategy.** Once the observer starts moving, optic flow becomes available. As the prism does not change the optical structure of the scene, the relative locations of the FoE and target remain unchanged. Therefore, walking to keep the FoE aligned with the target will result in a straight path to the target. (b) **Egocentric direction strategy.** The observer attempts to maintain the target straight-ahead and therefore has to realign the body to the seen target on each step. As the result, the trajectory is a curved (10° equi-angular spiral) path to the target. (c) Illustration of the curvature of a trajectory and the relative contribution of optic flow. Note horizontal axes stretched relative to vertical to aid visualization. Dark grey filled circle represents the target. Lightest orange line indicates a full curvature that is predicted by the sole use (100%) of egocentric direction with a 10° offset. Darker orange lines represent the trajectories with intermediate curvatures.

The use of virtual environments allowed the authors to assess how trajectory (and hence it was inferred, cue use) varied as a function of the visual complexity of the scene. It

was found that as the scene complexity increased, the trajectories straightened. It was concluded that the change in trajectory as the scene became more complex was due to an increase in the richness of the optic flow. The results were summarized with a model:

$$\frac{d\phi}{dt} = -k(\beta + wv\alpha) \quad [1]$$

where ϕ denotes the walking direction, k a turning rate constant, β the egocentric direction of the target (Rushton et al., 1998), α the visual angle between the focus of expansion and the target, or the *heading error*, v the walking speed, and w a measure of the richness of optic flow. The conclusion of the study, that "optic flow is used to guide walking", provided support for an extended version (to reflect the use of egocentric direction) of the original optic flow hypothesis. The results have subsequently underpinned work on optic flow and the visual guidance of walking.

Key to the interpretation of the study is the assumption that the difference in trajectory that was observed across the virtual environments was due to differences in the richness of optic flow. In Experiment 1, we test this assumption with four environments with varying richness of optic flow and measure the straightness of the trajectories (a measure of cue weight; see Equation 1).

Precision of heading judgement and the guidance of walking

If judgements of heading tap the same processes that guide walking (or under a stronger version of the hypothesis, if judgements of heading guide walking), there should be a relationship between the precision of heading judgements and the straightness of the walking trajectories. In standard cue combination models (Ernst & Banks, 2002; Hillis, Ernst, Banks, & Landy, 2002; Landy, Maloney, Johnston, & Young, 1995) the weighting given to a cue is dependent on the reliability of the cue. In an optimal combination model the weighting is based on the reciprocal of the variance (Ernst & Banks, 2002), which provides a way to operationalize the term w in equation 1. Therefore, the more precise the heading judgements are, the higher the weighting on optic flow, and in our experiment, the straighter the walking trajectories. Similarly, if the precision of the heading judgements changes between the beginning and end of the trajectory, this should be reflected in a change in the straightness of the trajectories.

In the first experiment we examine how well the richness of optic flow predicts the form of the walking trajectories in four environments (Figure 2). The data from the second

experiment allows us to examine how well the precision of heading judgements predicts the form of the walking trajectories. In our analysis we focus on rank order. Predicting rank order should be an easy test for any model, and hence a logical starting point before (if justified) progressing to quantitative predictions. We rank order the environments respectively on the basis of (1) the straightness of trajectories, (2) the richness of flow, and (3) the precision of heading judgements. Then we compare the order of trajectories to the other two orders. If the richness of optic flow predicts the general shape of the walking trajectories (Figure 1c), the order of the straightness of trajectories should be consistent with the order of the richness of optic flow. Similarly, if the precision of heading judgements predicts the shape of walking trajectories, the order of the straightness of trajectories should be consistent with the order of the precision of heading judgements.

Experiment 1: Walking trajectories.

We created four virtual environments (Figure 2) with progressively more optic flow (*Line* < *Outline* < *Room* < *Cloud*). Two of our environments were similar to environments used previously (Warren et al., 2001): the *Line* environment consisted of a high vertical line target, the *Room* environment was an enclosed space (room) made of solid surfaces painted with a random noise pattern, with a target doorway placed in the middle of the far wall (one difference from Warren et al, 2001, is that in their room environment there were no side walls). The *Outline* room environment was a line drawing version of the *Room* environment, with no enclosing surfaces. The *Cloud* environment consisted of a cloud of limited lifetime dots that filled the same volume as the Room, plus a line target.

Figure 2. Four environments and the availability of cues. **First column:** Environments shown from the start position. Horizontal field of view extended for illustrative purposes. The second and third column characterize the optic flow available in the four environments by simulating a viewer at 6m from the target moving forward but to the right of straight-ahead by 10°. **Second column:** Motion parallax between pairs of close points at different depths is key to identifying the direction of the translation from retinal flow in the presence of components of motion due to gaze rotations (Longuet-Higgins & Prazdny, 1980). The viewer's gaze was fixated at the target as indicated by the blue filled circle at the center of the image. Green crosses indicate the heading of the movement. Red arrows indicate motion parallax from neighbouring points at different distances (see Supplementary materials for details). Motion parallax is found in the Cloud environment but not the others (mean number of motion parallax vector pairs: Line: 0, Outline: 0, Room: 0, Cloud: 34). **Third column:** The FoE can be identified by finding the lowest speed in the image; or where the direction of motion reverses (Regan & Beverley, 1982). These points can be identified by comparing neighboring motion vectors or considering the global pattern across the whole image (for example by matching the flow pattern to templates, Perrone & Stone, 1994). The third column shows the distribution of image speeds in the four environments. The viewer's gaze was aligned with the moving direction, so the FoE corresponds to the heading. The interquartile range of speeds measured at a number of difference retinal eccentricities (1, 2, 5, 10, 15, 20, 30°, is approximately 2.5 times greater in the Cloud

environment than in the *Room* environment (see Supplementary materials for details). The greater range of speeds should stimulate a broader range of local and global motion detectors over a larger percentage of the walking step cycle and a larger range of walking speeds... The order of richness of optic flow (as defined by range of image speeds) is *Line* < *Outline* < *Room* < *Cloud*. **The fourth and fifth columns** characterize the scene boundaries that provide information about the allocentric location. The *Outline* and *Room* environments both contain edges. Only the *Room* environment includes bounding surfaces (i.e., walls, ceiling and floor). The sides of the *Cloud* may provide some very weak allocentric location information. The order of richness of allocentric location cues is *Line* < *Cloud* < *Outline* < *Room*. Egocentric direction, and its temporal derivative, target drift, is available, and comparable, in all four environments.

The *Line* environment contained no optic flow, the only cues to guide walking were the egocentric direction of the target (β in equation [1], Rushton et al., 1998), and the temporal derivative of egocentric direction, target drift (Llewelyn, 1971). The edges of the *Outline* environment added a minimal amount of optic flow. The *Room* environment added textured surfaces and so increased the amount of optic flow relative to the *Outline* environment.

The *Cloud* environment was an optimal optic flow stimulus. The flow vectors were evenly distributed throughout the environment and the retinal image. This is important for two reasons: (i) when the observer's eye rotates this adds a "confounding" component of retinal motion which complicates the identification of the focus of expansion, the direction of heading. Pairs of points that are at a similar location in the retinal image but at a different distance in space provide information about the direction of heading (Longuet-Higgins & Prazdny, 1980). The vector defined by the difference in motion of two neighboring points ("motion parallax", Longuet-Higgins & Prazdny, 1980), points to the direction of heading and so removes the consequence of eye rotations. There are no such pairs of points in the *Line*, *Outline* and *Room* environments but they are plentiful in the *Cloud* environment (see Fig2, second column). (ii) The range of image speeds was higher in the *Cloud* environment than in the other environments (see Figure 2, third column). The FoE can be identified by finding the lowest speed in the image; or where the direction of motion reverses (Regan & Beverley, 1982). These points can be identified by comparing neighboring motion vectors or considering the global pattern across the whole image (for example by matching the flow pattern to templates, Perrone & Stone, 1994). Local and global motion detectors in the brain are sensitive to motion at a range of speeds. The broad range of speeds in the *Cloud*

environment should stimulate a larger population of neurons, and continue to stimulate them over a larger portion of the step cycle when the instantaneous speed of motion of the observer changes.

On the basis of both (i) and (ii) we define the *Cloud* as the environment with the richest optic flow. The environments can be rank ordered as *Line* < *Outline* < *Room* < *Cloud* by optic flow. If the richness of the optic flow is the determinant of walking trajectory, we would expect the straightness of trajectories to follow the same order: *Line* < *Outline* < *Room* < *Cloud*.

The environments were carefully chosen so we could dissociate optic flow and non-optic-flow cues. We hypothesized the presence or absence of non-flow cues would upset the predicted order of trajectory straightness above. Consider the availability of *allocentric location cues* in the four environments. *Allocentric location cues* provide the observer with information about their location relative to the surrounding environment. Like optic flow, these cues would not be perturbed by prisms, and hence should help the observer take a straight trajectory towards the target. The *Line* environment lacks allocentric location cues. In the *Outline* environment, as the observer can locate herself relative to the room edges, the edges provide coarse allocentric location cues (Figure 2). Location relative to the surrounding space is most clearly specified in the *Room* environment, in which the observer can locate herself relative to the textured surfaces that bound and enclose the space. It is difficult for the observer to locate herself relative to the *Cloud* - the dots are located within a volume but the sides of the volume are hard to discern. The lack of correspondence between the richness of the non-flow cues (in the discussion above, allocentric location cues) and the flow cues across environments provides an opportunity to test how well the richness of optic flow predicts walking trajectories.

Method

In the experiment that follows we assessed how trajectories differ between environments. We derived two measures of trajectory, overall straightness (average over trajectory), and speed of straightening (how the trajectory changes) and take rank orders respectively according to these two measures. We compare the two orders to the order of richness of optic flow (*Line* < *Outline* < *Room* < *Cloud*).

Participants

It was necessary to recruit fifty-five participants, in order to obtain a counterbalanced sample, forty-eight in total (mean age = 19.5 [SD = 1.34] years, 7 males, normal vision or corrected to normal with contact lenses, no reported stereo, color vision or hearing impairments). Reasons for exclusion were technical faults during the experiment (N = 4) and outlier behavior (N = 3). Full details of exclusions are included in *Data analysis*.

Participants provided informed written consent and the research was approved by the School of Psychology research ethics committee. The participants were primarily psychology undergraduates participating for course credit. The difference in proportions of male and female participants reflects the difference in the undergraduate population. All were naïve to the actual purposes of the study, they were also unaware of the research on the visual guidance of walking (they had attended no course lectures or tutorials on the topic).

Apparatus and stimuli

All stimuli were generated in Vizard (WorldViz Inc., USA) on a laptop (weight ~5lbs) with GeForce GT 750M graphics chipset, and presented in an Oculus Rift DK2 (Oculus VR, USA) head-mounted display (HMD) with a nominal FOV of approximately 100° diagonally. The position and orientation of the participant's head were tracked by Impulse X2 motion capture system (PhaseSpace Inc., USA) at 480Hz. Data from the tracker was streamed wirelessly using the virtual-reality peripheral network (VRPN; Taylor II et al., 2001) protocol to the laptop that was carried by the participants in a backpack and connected to the HMD. This arrangement allowed the participant to walk freely without the distraction of trailing wires. The position and orientation data were used to update the images presented in the HMD at 75Hz. The system latency measured using a method similar to those reported by Morice, Siegler, & Bardy (2008) and Niehorster, Li, & Lappe (2017) was approximately 42ms. In addition, no perceivable latency was reported from participants.

A companion Vizard program running on a desktop PC was used to control the experiment progress and to record the position and orientation data sampled at 60Hz.

Virtual environments

The *Line* and *Room* environments were modelled on those used by Warren et al. (2001) with minor adjustments.

The *Line* environment (see column 1 of Figure 2) contained only a line target (height = 3m, radius = 0.02m). The bottom of the target was placed at the ground level. In this environment, the participant could only use the egocentric direction (β in equation [1], and its temporal derivative, target drift) of the target line to guide locomotion direction.

The *Room* environment (see column 1 of Figure 2) was a square room (12m×12m×3m) with the walls, floor and ceiling painted with a random-noise pattern. On the wall opposite to the starting point there was a doorway (2.5m high, 0.5m wide) surrounded by 5cm wide lines. The doorway served as the target.

The *Outline* and *Cloud* environments were created from the *Room* and *Line* environments.

The *Outline* environment was constructed by placing red lines at each of the edges of the room in the *Room* condition and then removing all the surfaces (i.e., walls, floor and ceiling). The width of the red lines was fixed to 2 pixels.

The *Cloud* environment was constructed by adding a cloud of 5250 white dots to the *Line* environment. The dots were uniformly distributed in the volume of space that is enclosed in the *Room* environment, resulting in an optic flow field comprised of a very rich set of velocity vectors. In line with previous work on optic flow, the dots remained a fixed size (diameter = 2 pixels), and to discourage the participants from tracking individual dots, the dots had a lifetime of 37 frames (approximately 0.5s at 75 frames/s).

An additional baseline environment was used in non-rotated trials (see next section) that were interspersed between the rotated trials in the four environments described above. The environment (see Supplementary Figure S1) consisted of a line target that was the same as in the *Line* condition and a flat ground plane with a horizon at 100m. The ground plane was painted with a random-noise pattern. A homogeneous black “sky” was rendered with the border at the horizon.

Design and procedure

Each participant completed 9 blocks, with each block containing four trials. In each even block, participants walked in one of the four test environments (Figure 2) and their virtual direction was either rotated rightwards (+10°) or leftwards (-10°) from the physical direction. Within each even block, the amount and direction of the rotation remained the same across the four trials. Across the even blocks, the rotating direction was alternated, and the order of the test environments was counterbalanced between participants. The odd blocks were baseline blocks in which the participants walked in the baseline environment

(Supplementary Figure 1) without any rotation between their virtual and physical directions. The first baseline block was treated as a practice to allow participants to familiarize themselves with walking in VR. The baseline block following each test block allowed us to measure any after-effects and to wash-out adaptation between conditions. The choice of four trials was based on an inspection of the data reported previously (Bruggeman, Zosh, & Warren, 2007). It was found that any adaptation built up over 38 trials was effectively abolished within four trials when a textured environment was used in the after-effect phase. We only had four experimental trials rather than 38 so we concluded four baseline trials would be sufficient.

In order to discourage the participants from paying undue attention to their walking behavior and guessing the real purpose of the study, a secondary task was used as a cover story. While walking to the target (line or door frame), participants could see the target color changing randomly between red, green and yellow every 0.75s (80 changes per minute). They were instructed to attend to the target and press the button on a wireless presenter every time the target turned to a specified color, e.g., red. The mean accuracy of the performance on the color change task was 96.5% (SD = 2.04%), and the mean response time is 451ms (SD = 38.3ms), suggesting that the participants were paying attention to the secondary task. In the debriefing session, none of the participants reported that they had been aware of the actual purpose of the study. In addition, none indicated being aware of the discrepancy between the visual and actual walking directions.

To help participants maintain their walking speed, a metronome was played to them via earphones. Participants were told that the metronome was to give them a sense of time in order to keep their walking speed constant. To avoid any confusion or discomfort, the metronome was played at 80 beats/minute, synchronized with the color changing of the target.

At the start of each trial, the participants stood 7m from the target and were asked to orient their body towards the target. When they were ready, the experimenter initiated the trial and then the participants started walking towards the target. They were instructed to walk through the target to finish the trial. When the trial was finished, the screen turned blank and the metronome stopped. The experimenter then turned the participants to the general direction of the target in next trial.

Participants took part in a brief prior experiment. The experiment involved walking to a physical target while wearing prism glasses (low angle displacement, high-quality lenses mounted in regular glasses frames). We combined the two experiments in the same session to reduce time demands on the participants and because we found that prior experience

wearing the tracking equipment and performing a similar attention task in the first experiment made participants more confident and comfortable in the primary VR experiment. Note we are confident of no carry-over effects for several reasons: (1) there was a gap between experiments; (2) the five trials with prisms were followed by five without to washout any after-effect; (3) there was no debrief; (4) the participants thought the first experiment was a familiarization phase for the second experiment; (5) there was a practice session at the beginning of the second experiment; and (6) the conditions in the first experiment were counter-balanced with respect to the condition order in the second experiment.

Data analysis

The participants' position data were first smoothed using a 2nd-order low pass Butterworth filter (MATLAB 2015b, the MathWorks, Inc., USA). The cut-off frequency for smoothing was individually determined for each participant based on their observed step frequency. Target-heading angle was calculated at each point on the smoothed position data as the angle between the current heading direction and the actual target direction. As in previous work (e.g., Warren et al., 2001), the beginning and end of each trial (here before 0.5m and after 6m) were excluded from further analysis because of the large amount of noise in calculating target-heading angle due to slow walking at the beginning and end of the trial. From the remaining dataset of 5.5 m, we calculated the mean target-heading angle for each trial.

The participants walked at their own speed, so the amount of data collected varied. We normalized the trajectories by dividing the trajectories into 100 segments of equal length along the z-axis. Means were calculated for each segment, and segments were averaged across trials and participants.

Any data point with a target-heading angle more than 10° from the expected range of 0°-10° was excluded. Also, data from individual trials were excluded as a whole if the overall mean target-heading angle for those trials was more than 10° from the expected range of 0°-10° (a total of five out of 1835 trials), or more than three SDs from the mean over all participants (a total of different five trials out of 1835 trials). If the excluded trial was the first trial in each block, then all the data from the participant was removed from subsequent analyses. A total of three participants were removed.

All statistical analyses were run using R (version 3.2.4). To compare the overall straightness between conditions, analyses were conducted on the overall mean target-heading angle averaged over the distance (5.5m) across the four test trials and participants. Repeated-

measures analysis of variance (ANOVA) was used to compare the difference between the conditions. Greenhouse-Geisser correction was used in the case of sphericity violation. To evaluate the rate of straightening of trajectories with the distance, linear mixed models were built on the target-heading angles against the distance to the target (or *growth curve analysis*, see Mirman, 2014), including fixed effects for *environment*, and random intercept (target-heading angle at 2m) and random slope (change of target-heading angle against distance) for individual participants. The rate of straightening was calculated as the slope parameter in the model. Statistical significance of the fixed effects was calculated following a standard protocol as suggested by Singer and Willett (2003; see Supplementary Materials for more details). All growth curve analyses were carried out in R using the *nlme* package (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2017) and *multcomp* package (Hothorn, Bretz, & Westfall, 2008) for simultaneous comparisons of differences between environments.

Results

Participants walked four trajectories in each environment. The data from the first trial best captures the on-line use of optic flow in the visual guidance of walking; in later trials, adaptation may have occurred (we return to this issue later). The first trial mean trajectories and target-heading angles against distance are plotted in Figure 3 (panels a and b respectively). For statistical analysis, we first collapsed over distance and compared means across environments; we then examined how behavior changed as a function of distance.

Figure 3. Mean trajectories and mean target-heading angles as a function of distance. (a) Mean trajectory and 95% confidence intervals on Trial 1 for Line (thin light blue), Room (green dot-dashed), Cloud (orange dotted) and Outline (purple dashed). Long-dashed grey line illustrates the

trajectory if only egocentric direction is used. Shaded areas represent 95% confidence interval. (b) Mean target-heading angle as a function of distance on Trial 1, for Line (thin light blue), Room (green dot-dashed), Cloud (orange dotted) and Outline (purple dashed). Long-dashed horizontal line at 10° indicates the angular offset between the virtual and physical directions. Shaded areas represent 95% confidence interval.

As is evident in Figure 3b, there was a significant difference in the mean target-heading angle (proportional to the overall curvature of the trajectories and opposite to the straightness of trajectories) between the environments [$F_{3, 141} = 18.56$, $p < 0.001$, $\eta_p^2 = 0.28$] on Trial 1. The trajectory in the *Line* environment was less straight (higher target-heading angle) than the other three environments [Mean = 9.86° , SD = 2.82; all $ps < 0.05$, Bonferroni correction]. The trajectories in the *Room* environment were the straightest (least curved and lowest target-heading angle) [Mean = 5.48° , SD = 2.45; all $ps < 0.01$, Bonferroni correction]. In the *Cloud* and *Outline* conditions, the overall curvature of the trajectories was similar [*Cloud*: Mean = 7.67° , SD = 3.08; *Outline*: Mean = 7.99° , SD = 2.76; $t(47) = -0.51$, Bonferroni-corrected $p > 0.5$]. We can summarize the results as *Line* < (*Cloud* $\approx$ *Outline*) < *Room*. This ordering does not reflect the richness of optic flow in the four environments.

Next, we looked at the speed of straightening of trajectories by examining the rate of change of target-heading angles as a function of distance. Across the first trial, the target-heading angle changed at different rates (calculated as the slope of regression line over the distance from 6m to 2m using growth models, Mirman, 2014) in the four environments (see Figure 2b) [$\chi^2(3) = 21.30$, $p < 0.0001$; see Supplementary Materials]. The slowest decrease was in the *Line* environment, the estimated slope was not statistically different from $0^\circ/\text{m}$ [estimated slope = $-0.28^\circ/\text{m}$, $p = 0.12$]. In contrast, the target-heading angle decreased significantly in all other environments [estimated slopes $< 0^\circ/\text{m}$, Bonferroni-corrected $ps < 0.0001$]. The most rapid decrease in the target-heading angle was in the *Outline* environment [estimated slope = $-1.46^\circ/\text{m}$, significantly $>$ *Cloud* and *Line*, both Bonferroni-corrected one-tailed $ps < 0.05$; marginally $>$ *Room*, Bonferroni-corrected one-tailed $p = 0.07$]. The rate of decrease in target-heading angle was comparable in the *Cloud* [estimated slope = $-0.75^\circ/\text{m}$] and *Room* environments [estimated slope = $-0.90^\circ/\text{m}$; $p = 0.54$]. We can summarize the results as *Line* < (*Cloud* $\approx$ *Room*) < *Outline*. Again, this order does not reflect the richness of optic flow in the four environments^{‡§}.

[‡] It could be argued we should have used a different distance range for analysis to the one used (6-2m). As the the lines in Figure 3, panel B are not straight, the choice of distance

In summary, neither the overall straightness nor rate of straightening of walking trajectories reflects the richness of optic flow in the four environments.

Experiment 2: Heading judgements.

The results of the first experiment indicate that the richness of optic flow does not predict walking trajectory. In the second experiment we examine how well the precision of heading judgements predicts walking trajectories.

Participants performed heading judgements at four simulated distances, 7m, 6m, 5m and 3m from the target. We assumed that while participants processed and responded to heading information, they would have travelled ~1m (typical step distance is ~0.35m for population used). Therefore, we compared the heading judgements to target-heading angles between 6m and 2m from the target. Note, 1m for processing and responding is not critical; the same pattern of results was found when we checked 0.5m or 1.5m travel distance.

If the precision of heading judgements predicts the shape of walking trajectories, we should expect to see both the orders of overall straightness, and speed of straightening, of trajectories to be consistent respectively with the orders of the overall precision of heading judgements, and the change in precision of heading judgements, across the distances to the target.

It is not possible to collect both the walking and judgement data at the same time. One task has to precede the other. Is it better to collect walking data first or second? Arguments can be made both ways. We resolved this question by bracketing the collection of walking data, collecting half of the data on participants who had completed the walking task (Experiment 1), and half on participants who had not. This allowed us to check for

range could change the ordering of the conditions or the statistical differences between them. We checked the impact of choice of distance range by examining 12 different ranges (6m-1m, 6m-1.5m, 6m-2.5m, 6.5m-1m, 6.5m-1.5m, 6.5m-2m, 6.5m-2.5m, 5.5m-1m, 5.5m-1.5m, 5.5m-2m, 5.5m-2.5m, and the original 6m-2m). The ordering of conditions was robust. In only 1 range (6.25m - 2.5m) of the 12 was the slope in the Outline environment not the largest (Slopes: Line = -0.30, Cloud = -0.78, Outline = -1.19, Room = -1.20). But even with that range, our conclusion stands, the ordering of environments by walking trajectory does not reflect the richness of optic flow.

[§] Our participant sample had more female participants (41) than male participants (7). We examined the male and female data separately (see Supplemental Materials). In brief we found that male participants walked less straight trajectories than the female participants in the Cloud and Line conditions. If our sample is representative then the behavior of male participants poses an even greater challenge than the behavior of female participants.

statistically significant differences between the two halves of the dataset and also collect what we believed would be the most representative judgement data.

Method

Participants

Participants were recruited from the same population as Experiment 1. Participants were recruited until, after necessary exclusions, we had a counterbalanced sample, twenty-four in total (mean age = 19.8 [SD = 1.58] years, five males, normal vision or corrected to normal with contact lenses, no reported stereo, color vision or hearing impairments). In order to obtain these numbers, we had to recruit twenty-eight participants. One participant did not finish the experiment due to nausea. Data from three participants were removed. Full details of exclusions are included in *Data Analysis*.

Participants provided informed written consent and the research was approved by the School of Psychology research ethics committee. All were naïve as to the actual purposes of the study.

Apparatus and equipment

The same four virtual environments were created and presented in the same way as in Experiment 1. Participants were asked to view a simulated movement through the virtual environments and to make a judgement of the direction of the simulated movements. The participants were seated and wearing the same HMD as used in Experiment 1. The orientation of the participant's head was monitored using the built-in trackers of the HMD and the view of the scene was updated to reflect current head orientation.

Simulated movements

Translation of the observer through the virtual environment was computer controlled. Translation speed was 0.75m/s (the mean walking speed in Experiment 1 was 0.73m/s) for a duration of 1s, with a translation direction to one side of the target. The translation, or heading, direction started 5° away from the target and then reduced using an adaptive staircase (Kesten, 1958) to identify the heading direction at which the likelihood of correctly judging translation direction (left or right of the target) reached 75%. The direction of the translation (left or right of the target) was randomly chosen on each trial. Simulated translation began 7m, 6m, 5m or 3m from the target. The four different scenes and four different start distances were randomly interleaved. There were 25 trials at each distance, in

each scene, making for 400 trials in total (25 test trials $\times$ 4 distance conditions $\times$ 4 scene conditions).

Design and procedure

The participants' task was to click the corresponding arrow key on a keyboard to indicate if the translation was to the right or left of the target. To provide a check of whether the participants were paying attention to the task, and to keep the participants motivated, 15 catch trials were intermixed with the test trials in each scene condition. The catch trials were designed to be very simple. The heading angle was fixed at 10°, and the starting distance was 3.5m from the target. Over 75% of the participants achieved an accuracy greater than 98.3% (meaning that they got one trial wrong at most). Data from three participants whose accuracy on the catch trials was lower than 96.6% (more than two trials wrong) was excluded.

At the beginning of the experiment, each participant was given 12 practice trials with feedback to become familiar with the experimental procedure. For all the practice trials, the baseline environment was displayed.

Each trial started with the head pointing straight-ahead of the body. Once the simulated movement began, participants were allowed to turn their head (e.g., to align their head with the target).

Data analysis

The responses were fit with a cumulative Gaussian and the threshold was defined as the distance between the 75% and 25% points on the curve. Group means were calculated with data points further than 3 SDs from the mean excluded from the final analysis (none were outside 3 SDs from the mean). Repeated-measures analysis of variance (ANOVA) was used to compare the difference between the conditions. Greenhouse-Geisser correction was used in the case of sphericity violation. To evaluate the change of precision of heading judgements as a (linear) function of distance to the target, a growth model was built on the thresholds (Mirman, 2014; see Supplementary Materials for details).

We compared the pattern of heading judgement of participants that had performed the walking experiment first (Experiment 1) to those that had not. There was no significant difference between the two groups (see Supplementary Materials for details), so we collapsed the two groups in the final analysis.

Results

Collapsed over distance, the mean thresholds (and 95% CIs) were, in order: *Line* = $1.59^\circ \pm 0.41^\circ$, *Outline* = $1.59^\circ \pm 0.20^\circ$, *Room* = $1.09^\circ \pm 0.14^\circ$, *Cloud* = $1.01^\circ \pm 0.17^\circ$ (see Figure 4a). Thresholds of $1\text{--}2^\circ$ are comparable to those typically reported on judgements of heading with displays with rich optic flow (e.g., Warren et al., 1988). Repeated-measures ANOVA showed that the differences between the environments were statistically significant [$F_{1.58, 36.29} = 9.88$, $p < 0.001$, $\eta_p^2 = 0.31$]. The heading judgements were less precise [all $ps < 0.01$] in the *Line* and *Outline* environments than in the *Cloud* and *Room* environments. The precision was very similar in the *Line* and *Outline* environments [*Post-hoc* test with Bonferroni correction, $p > 0.5$], and in the *Cloud* and *Room* environments [$p > 0.5$]. This ordering ($\text{Line} \approx \text{Outline}$) $<$ ($\text{Cloud} \approx \text{Room}$) based on mean thresholds does not fit well with the ordering of the walking data from Experiment 1: $\text{Line} < (\text{Cloud} \approx \text{Outline}) < \text{Room}$.

A visual comparison of the patterns of walking trajectories in Experiment 1 (Figure 3a) and the precision of heading judgement here (Figure 4a) highlights stark differences between the two. In Experiment 1, the walking trajectories in the *Cloud* were notably more curved than those in the *Room* environments, and the trajectories in the *Outline* environment were significantly straighter than in the *Line* environment (Figure 3a). However, the precision of heading judgement was similar between the *Cloud* and *Room* environments, and between the *Outline* and *Line* environments (Figure 4a).

Figure 4. (a) Mean threshold averaged across four distances for each environment. Error bars indicate 95% confidence interval. (b) Mean threshold for each virtual environment for each distance

(7, 6, 5, 3m). Position of four curves jittered to aid readability. Error bars indicate 95% confidence interval.

The slope of the function (threshold against distance) captures how the precision of the heading judgements change as the observer gets closer to the target. The slopes were calculated using growth modelling (Mirman, 2014; see Supplementary Materials). In order, the mean slopes were: *Line* = $-0.34^{\circ}/\text{m}$, *Outline* = $-0.18^{\circ}/\text{m}$, *Cloud* = $-0.02^{\circ}/\text{m}$ and *Room* = $0.05^{\circ}/\text{m}$. The increase in precision (reduction in threshold) was statistically significant in the *Outline* and *Line* environments (slopes significantly smaller than $0^{\circ}/\text{m}$, both $ps < 0.01$), but not in the *Room* and *Cloud* environments [slopes not statistically different from $0^{\circ}/\text{m}$, both $ps > 0.5$]. There were significant differences between these slopes [$\chi^2(3) = 31.41$, $p < 0.001$]. The differences reached statistical significance between the *Line* environment and both the *Room* and *Cloud* environments [*Post hoc* tests with Bonferroni corrections, both $ps < 0.0001$]. We can summarize these results as $(\textit{Line} \approx \textit{Outline}) > (\textit{Room} \approx \textit{Cloud})$ (noting the statistical significance of the differences above). These results can be compared to the change in straightness in the walking data from Experiment 1, $\textit{Line} < (\textit{Cloud} \approx \textit{Room}) < \textit{Outline}$. Again, the trajectory and judgement data do not mirror each other.

Longer term impact of optic flow on visually guided walking

To this point we have found that neither the richness of optic flow, nor the precision of heading judgements, predicts walking trajectory. However, our analysis focused on the first trial trajectories. Before concluding, it is important to look further. Richness of optic flow may prove a good predictor of trajectory over a longer time frame: Exposure to discrepant visual feedback (as happens in our experiment) leads to a process of adaptation, either of perception (Rushton & Salvucci, 2001; Herlihey & Rushton, 2012), and/or of perceptual-motor mappings (Bruggeman et al., 2007). Such an adaptation would change the trajectories taken. We assessed the impact of the richness of optic flow on longer-term walking trajectories by comparing changes in trajectory from the 1st to 4th trials in the four environments (Figure 5).

Figure 5. Mean target-heading angles of the early and the later parts of the trajectory as a function of trial. (a) Mean target-heading angles of the early (red) and the later (blue) parts as a function of trial for the four test trials. Dashed lines at 10° indicate the angular displacement between the visual and movement direction. Error bars indicate 95% confidence interval. (b) Mean target-heading angles of the early (red) and the later (blue) parts of the trajectory as a function of trial for the four baseline trials. Error bars indicate 95% confidence interval.

We first examined the target-heading angles for the early (6 ± 0.25 m from the target) part of the trajectories (Figure 5). Changes in the early measure indicate adaptation (as for example would result from changes in perceived egocentric straight-ahead, Herlihey & Rushton, 2012). The mean target-heading angle of the early part of the trajectory reduces from the first to the fourth trial in all environments [all Bonferroni-corrected $ps < 0.05$], indicating adaptation. The reduction from the first to fourth trial was, in order of magnitude,

3.02° (SD = 3.19°) in the *Cloud* environment, 1.99° (SD = 4.23°) in the *Room*, 1.33° (SD = 3.26°) in the *Outline* and 1.28° (SD = 3.29°) in the *Line* environment. This ordering (*Line* < *Outline* < *Room* < *Cloud*) does reflect the richness of optic flow across environments and is compatible with earlier work (Herlihey & Rushton, 2012).

We can examine further this pattern by looking at after-effects. Once the 10° offset is removed, participants' trajectories should initially be displaced in the opposite direction. Figure 5b shows the target-heading angle in the four trials in the baseline environment (ground plane; see Supplementary Figure S1) that immediately follow the four test trials. A significant after-effect, as indicated by the negative mean target-heading angles in the early part of Trial 1 of baseline blocks in Figure 4b, is observed following all environments except the *Line* environment [all Bonferroni-corrected one-tailed $ps < 0.01$, except *Line*: $t(47) = -1.15$, Bonferroni-corrected one-tailed $p = 0.25$]^{**}. The ordering of the magnitude of the after-effect across environments mirrors the ordering of the change in early target-heading angle in the experimental environments: *Line* < *Outline* < *Cloud* < *Room*. This ordering also reflects the richness of the optic flow.

Further evidence of a role for non-flow cues in the online guidance of walking

As already noted, changes in trajectory between early and late (2 ± 0.25 m from the target) parts of the trajectory provide insight into the use of cues for online guidance of walking. In Trial 1, the largest change in trajectory was found in the *Outline* environment. This is particularly noteworthy because the *Outline* environment contains minimal optic flow, which suggests a cue other than optic flow is contributing to the online guidance of walking. Trials 2-4 provide the opportunity to examine whether the pattern in the first trial persists. It does. Across Trials 2-4 (Figure 5), trajectories straighten up (mean target-heading angle decreases) from the beginning (red squares in figure 5) to the end (blue circles in figure 5) of the trajectory. The changes occur at different rates in the four environments for Trial 2 ~ Trial 4 [$\chi^2(1) = 91.26$, $p < 0.001$]; the change (distance between red squares and blue circles in Figure 5) is smallest in the *Line* environment [mean reduction = 1.79°, SD = 2.99°] and largest in the *Outline* environment [mean reduction = 3.28°, SD = 3.29°].

^{**} Based on earlier data (Bruggeman et al., 2007) we assumed that the after-effect would be abolished after 4 trials. While this is true in general, the later target-heading angle measures suggest a small residual after-effect may remain on the final trial after both the *Room* and *Cloud* conditions (because we used a fully counter-balanced design this should not impact on the comparisons between the *Line*, *Cloud* and *Outline* conditions, though it may slightly decrease the apparent straightening in those conditions [by approx. $\frac{1}{3}^\circ$]).

General Discussion

Our goal was to examine two assumptions about the role of optic flow and heading judgements in the visual guidance of locomotion: (1) that the richness of the optic flow predicts walking trajectories; and (2) that judgements of heading measure the information used in the visual guidance of walking. We review the compatibility of our data with the two assumptions.

Does richness of optic flow predict walking trajectories to a seen target?

In Experiment 1 we recorded the trajectories of participants walking to seen targets when there was an angular offset between seen and movement direction. The predicted ordering of environments if participants' behavior (straightness of walking trajectories) was determined by the richness of the optic flow is *Line* < *Outline* < *Room* < *Cloud*. We found *Line* < (*Cloud* $\approx$ *Outline*) < *Room*. Most notably, the *Cloud* environment provided the richest optic flow (Figure 2) and therefore the trajectories should have been the straightest. They were not. The similarity in mean target-heading angle in the *Cloud* and *Outline* environments poses a further challenge given the marked difference in optic flow in these environments (Figure 2).

It is difficult to reconcile these results with the assumption that differences in optic flow account for differences in trajectory in a visually richer environment. One solution would be to “define away” the findings. In Gibson’s original writings optic flow was used as a shorthand for all changes in visual input over time^{††}, the results would be compatible with such an all-compassing definition of optic flow. The problem with the “definitional” solution is that optic flow has a very clear meaning today that is independent of Gibson. Seminal mathematical (e.g. Koenderink, 1986), behavioural (e.g. Warren & Hannon, 1988) and neurophysiological papers, equated optic flow with the instantaneous pattern of motion (vector field) available at the eye, and that definition has held since. The definition underpins historical debates, (e.g., optic flow versus differential motion parallax, Cutting et al, 1992) and has been adopted in other communities, most notably in the field of computer vision which now produces the majority of published papers on optic flow. The ubiquity of the contemporary definition is illustrated by a simple internet search (see results of an Image or General search using Google). The other problem with the “definitional solution” is that if

^{††} We thank an anonymous reviewer for pointing this out to us.

optic flow is defined as all changes in the optic array over time, the term becomes all-encompassing and hence redundant.

Do heading judgements tap the visual information used in the visual guidance of walking?

The mean precision of the heading judgements followed the order (*Line* $\approx$ *Outline*) < (*Cloud* $\approx$ *Room*). If the mean precision of heading judgements predicts walking trajectories, then the order of the straightness of trajectories should be the same as the order of the precision of heading judgement. However, the prediction fails, the order of the straightness of trajectories when walking was *Line* < (*Cloud* $\approx$ *Outline*) < *Room*.

The change in the precision of heading judgements from far from the target to close to the target followed the order (*Line* $\approx$ *Outline*) > (*Cloud* $\approx$ *Room* $\approx$ 0). The change in mean target-heading angle from far to close to the target was *Line* < (*Cloud* $\approx$ *Room*) < *Outline*, which is, again, different from the order of change in the precision of heading judgements.

Vivid illustrations of the stark differences between trajectories and judgements are (i) between the slopes in the *Line* environments in the two experiments, and (ii) between the slopes in the *Room* environment in the two experiments.

Given the marked differences between the patterns of heading judgements and walking trajectories it is difficult to reconcile the results with an assumption that heading judgements tap the same information that is used in the visual guidance of walking. This conclusion is in line with other work that found differences between heading judgements and steering (Kountouriotis & Wilkie, 2013; Wilkie & Wann, 2003).

Long-term impact of the richness of optic flow on walking trajectory

When we found that the richness of the optic flow did not predict walking trajectories in the initial analyses we looked further. We found evidence that the richness of optic flow is important over a longer period of time. The changes in the initial trajectory direction over trials, and the magnitude of the after-effects (*Line* < *Outline* < *Room* < *Cloud*), are predicted by the richness of the optic flow across the different environments.

Evidence for a role for allocentric location cues in the visual guidance of walking?

Our experiments dissociated the richness of flow and non-flow cues across four environments. This allowed us to test how well the richness of optic flow and precision of heading judgements predict walking trajectory. The non-flow cues we manipulated were allocentric location cues. The fact that we found that their richness had an impact on walking trajectories points to their use in the visual guidance of walking. We think the most interesting feature of the data is the straightening that occurs between the beginning and end of the trajectories in the *Cloud* and *Outline* environments. Straightening indicates the online use of information in the guidance of walking. The *Outline* condition contains only edges which provide coarse perspective-based geometric cues. Across all four trials there was more straightening in the *Outline* condition than the *Cloud* condition.

Previous work demonstrated the potential role of allocentric location cues in judgements of heading (Beusmans, 1998; Hahn, Andersen, & Saidpour, 2003; Vishton & Cutting, 1995), and on the basis of those results the authors concluded that allocentric location cues would likely have a role in guiding walking. Although we find here that heading judgements are not predictive of walking behavior, the suggestion that allocentric location cues have a role in guiding walking fits with our results.

The findings we report here provide a foundation for work to directly test the role of allocentric location cues in the visual guidance of walking.

Conclusions

Taken together, the results of the experiments reported here challenge assumptions about optic flow, perception of heading and the visual guidance of locomotion. Neither the richness of the optic flow nor the precision of heading judgements predicts walking trajectories. Furthermore, the results suggest an important role for allocentric location cues in the visual guidance of walking.

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