Allocentric location cues and the visual guidance of walking towards seen targets

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Abstract

We hypothesised allocentric location cues (information about the location of an observer relative to the surrounding environment) have a role in the on-line visual guidance of walking towards seen target objects. We used a standard technique for assessing the contribution of cues when walking to targets: we perturbed the perceived egocentric direction of the target, and measured the curvature of the resultant walking trajectories. By removing motion cues we were able to isolate allocentric location cues and quantify their utility. Enclosed, geometrically regular, environments contain rich allocentric location cues. In the first experiment participants walked through a large enclosed outdoor space; allocentric cues were isolated by synchronised eye closing and stepping. In the second experiment participants walked through a smaller enclosed indoor space; allocentric cues were isolated with stroboscopic lighting. Both experiments provided support for the hypothesis that, when they are available, allocentric location cues have a key role when walking to seen targets.

Keywords: Walking; optic flow; allocentric location; egocentric direction; visually guided action; perception and action

1.0 Introduction

An extensive body of neurophysiological work has shown that a rodent's location relative to its surrounding environment, its world-relative location, or *allocentric location*, is coded in spatially-responsive neurons in the hippocampal formation and surrounding neural areas (Moser, Kropff & Moser, 2008) (O'Keefe and Dostrovsky, 1971). Evidence suggests a comparable neural representation of allocentric location in humans (Doeller, Barry, & Burgess, 2010; Ekstrom et al., 2003; Jacobs et al., 2013; Miller et al., 2013) and it has been reported that scene-selective neural areas code the distance and orientation of large surfaces (Lescroart & Gallant, 2019).

Here we examine the role of allocentric location cues in the online visual guidance of walking to a seen target. To date, research has focussed on two sets of cues: visual motion cues, and egocentric direction cues. The most well-known motion cue is optic flow (Gibson, 1954/2009, 1958/1994). When an observer moves forward a radial pattern of optical motion is created at the eye (Figure 1a). The centre of the radial pattern indicates the direction of translation (the "heading" direction). Other prominent motion cues include differential motion parallax (Cutting et al, 1992) and target drift (the motion of the target relative to the observer, or a point fixed relative to the observer; Llewellyn, 1971). Egocentric direction (Rushton, Harris, Lloyd and Wann, 1998; Figure 1b) is the direction of the target relative to the observer's body: if the observer regulates locomotion direction to keep the target at a fixed direction, typically straight ahead, he or she will reach the target.

We hypothesised that allocentric location cues play a role in not just navigation to an unseen target and path integration (e.g. Bush, Barry, Manson & Burgess, 2015), but also in the visual guidance of walking to seen targets.

Figure 1. ***a.** Radial optic flow field, the pattern of motion available at the eye of an observer moving forward. An observer would reach a target by keeping the centre of the flow field over the target object. **b.** Egocentric direction, the direction of an object relative to the body. An observer would reach a target by walking so as to keep the target perceptually straight ahead, i.e. at $\alpha=0$.*

The use of allocentric location cues in the visual guidance of walking is hinted at in existing studies. In the published research there has been disagreement about the contribution of optic flow and egocentric direction cues. A common feature of studies that report evidence for use of optic flow, is the use of geometrically regular enclosed environments (e.g., Warren et al., 2001; Turano, Yu, Hao, & Hicks, 2004). A common feature of those that do not report evidence for use of optic flow is the use of open and irregularly shaped environments (e.g., Rushton, et al, 1998; Saunders, & Durgin, 2011). The more plentiful allocentric location cues in the enclosed environments could explain the difference.

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Figure 2: *Perspective cues in the retinal images that provide information about allocentric location.* **a.** The angle formed by the bottom of two side walls and the far wall (see splay angle; Beall and Loomis, 1996), is informative about lateral position. In the left image the observer is located halfway between the walls, in the right the observer is located towards the left. **b.** The perspective shape of an interior corner is informative about position relative to the corner (Beusmans, 1997). In the left image the observer is located directly ahead of the corner, in the right image the observer is stood to the left. **c.** Perspective shape of a wall. In left image observer is located at central location facing the wall. In the right image, the observer is stood to the right, facing to the left.

56

57 Observers could use a variety of sources of visual information to infer allocentric
 58 location, such as the distances to surrounding walls. A particularly rich source of
 59 information on allocentric location comes from perspective cues. For example, lateral
 60 position in a room or corridor, is indicated by the visual angles of the lines formed by

61 the bottom edges of the left and right walls in the retinal image (splay angle; Beall
62 and Loomis, 1996; Figure 2a). The relative image size of the left and right walls (or
63 texture or features on the walls) also provides information about lateral position.
64 Position relative to a corner is indicated by the perspective shape of the image of the
65 wall (Figure 2b; Beusmans, 1997). Orientation relative to a wall ahead is indicated by
66 the perspective shape of the wall (Figure 2c) in the retinal image.

67 We have highlighted perspective cues here for illustrative purposes but other cues
68 could provide information about allocentric location. For example, absolute and
69 relative distance cues (see Cutting & Vishton, 1995 for an overview of cues to
70 distance) provide information about the position of the observer relative to the
71 surrounding environment.

72 To reach a seen target using allocentric location cues, the observer would monitor and
73 regulate their location relative to the surrounding environment, using allocentric
74 location cues - rather than monitoring motion, or egocentric direction cues.

75 We designed an experiment to test our hypothesis that allocentric location cues
76 provide important information for the visual guidance of walking to a seen target. We
77 used prism glasses (a standard tool that rotates the visual scene to the left/right
78 relative to the observers' head) to selectively perturb the perceived egocentric
79 direction of a target ~17m away (see Figure 3). If no cues other than egocentric
80 direction are used the observer would take a predictable curved trajectory to the target
81 (Rushton et al, 1998). If the trajectory is straighter than the "egocentric trajectory"
82 then this indicates other cues are playing a role. The straightness of the trajectory
83 indicates the strength, or contribution, of the other cues.

84 The first group (“Motion” condition) of participants walked normally through a
 85 typical modern urban enclosed environment to a seen target with both motion and
 86 allocentric location cues available. The second group (“StopGo” condition) paused
 87 between steps which made the motion cues discontinuous. The third group
 88 (“NoMotion” condition) only opened their eyes when they were stationary between
 89 steps and so saw a series of “snapshots” of the environment. This removed motion
 90 cues completely but allocentric location were still available when the eyes were open.
 91 We were thus able to compare trajectories in which only allocentric location cues
 92 were available with natural walking trajectories in which full cues were available.

Figure 3: (a) and (b) Base right, leftward displacing prisms. Both (c) and (d) show the experimental area. (c) was taken through the leftward prisms shown in (b). (d) was taken without prisms.

93

94 The animal literature suggests that the neural coding of location stabilises over time
 95 (Frank et al. 2004), therefore we measured walking over an extended period, 48 trials,
 96 to see if the trajectories changed. However, to be able to assess if there was a change
 97 in the use of allocentric location cues it is necessary to account for changes that occur

in perception of egocentric direction. In earlier work (Herlihey & Rushton, 2012) we found that perceived egocentric direction changes after walking with prisms in the same environment. So we could factor out any changes in trajectory due to changes in perceived egocentric direction, and isolate any change due to use of allocentric location cues, we inserted measures of perceived straight-ahead into the experiment.

To anticipate the results, in the NoMotion condition we found trajectories were less curved than would be expected if egocentric direction was the sole cue used. This suggests that allocentric location cues provide valuable information for the visual guidance of walking to a seen target. In addition, the presence of motion cues (continuous or discontinuous) had little impact, which raises questions about the role or necessity of motion cues.

Experiment 1 was conducted in an outdoor space. We tested, and supported, our key conclusion about the role of allocentric location cues in a replication, Experiment 2, which was conducted in a large room, using a strobe lighting to isolate allocentric location cues.

2.0 Experiment 1

2.1 Methods

2.1.1. Participants

Sixty-five (11 male) right-handed healthy participants with normal, or corrected to normal (by contact lenses only) vision from Cardiff University took part in return for course credit. Five participants were unable to complete the experiment due to weather conditions (the experiment took place outside). The remaining sixty participants were evenly split across three conditions (see below). The research was

carried out in accordance with the Declaration of Helsinki, all participants gave informed consent and the School of Psychology's Ethics Committee approved the study.

As there is no prior research that addresses the question we were interested in we were unable to perform an a priori power analysis, therefore for Experiment 1 we were guided by prior literature. Previous research by Bruggeman & Warren (Bruggeman, Zosh, and Warren, 2007; Bruggeman and Warren, 2010) used 16 or 20 participants, others have used fewer, e.g. Saunders and Durgin (2011) and Rushton et al (1998). We chose to go with the largest group size, 20 participants per condition. We use 95% CIs to convey the precision of the measurements and Bayes Factors to evaluate the relative weight of evidence for and against differences.

2.1.2. Experimental setup

Participants walked within an outdoor environment (see Figures 3 and S1). Four buildings enclosed the space. A number of objects, including plant pots, benches and bicycle racks were arranged around the edges of the environment.

To produce a shift in the perceived direction of the target object, participants wore high quality, custom made, binocular prism glasses (see Figure 3) that produced a lateral rotation of 8.5°. For each condition, ten participants wore base left, rightward displacing prisms, and ten wore base right, leftward displacing prisms.

Three target posts were located at one end of a 17 x 5 m rectangular area (Figure S1), and two were located at the opposite end. Luminous material was attached to the posts a little below eye height (1.5 m). Participants were required to walk back and forth between the posts as instructed by the experimenter while maintaining fixation on the luminous material (see Procedure).

2.1.3. *Experimental conditions*

The three conditions (Motion, StopGo, NoMotion) were described briefly above. In the Motion condition participants walked at a natural pace to the target. This condition allowed us to assess how people walk normally in a typical full cue environment and it served as a reference for comparison. The StopGo condition required the participants to bring both feet together after each step, and pause momentarily, before proceeding. This condition allowed us to determine the effect of discontinuous stepping, and hence optic flow. In the NoMotion condition, participants performed the same stepping actions as in the StopGo condition but they *only opened their eyes while they were stationary* (i.e., eyes were closed while stepping towards the target and only open when pausing between steps). This condition was the one of primary theoretical interest as it removed optic flow while preserving the allocentric location cues. Further information on the visual information available in the StopGo condition is provided in the supplemental materials [see HerliheySM.pdf].

2.1.4. *Procedure*

At the beginning of the trial the participant closed his or her eyes before donning the prism glasses. Next, with eyes closed, the participant was rotated 1.5 times so that he or she was facing in the general direction of the target (located at the other end of the rectangular area, at a distance of approximately 17 m). This routine was used to (i) prevent participants from seeing a shift in visual direction that would have been apparent if they put on the prism glasses while stood still with eyes open, and (ii) prevent participants from correcting for the displacement of the visual image with a change in head orientation. The experimenter informed the participant of their target, then, with eyes open, the participant turned and faced the target before the trial began.

Each participant walked 48 trajectories in total, taking on average 40 minutes to complete the experiment, walking a total of approximately 770 metres. Measures of perceived straight-ahead (see below) were taken without prisms prior to initial exposure, and after four phases: phase 1, after 6 trajectories: phase 2, after a further 6 trajectories (total 12): phase 3, after a further 12 trajectories (total 24): phase 4, after a further 24 trajectories (48 in total). After each phase, the participant was asked to close his or her eyes and was guided to the ‘measurement area’ located approximately 5 m away from the walking area (Figure S1); measurements of straight ahead were then re-taken. After the measurements, with eyes closed, the participant was guided back to the ‘walking area’.

2.1.5. Measurement of walking trajectories

Head and target position were recorded in a plan view using a Sony Ex Wave HAD colour video camera (running at 50 Hz), mounted on the twelfth-floor balcony of one of the surrounding buildings. The videos were processed using custom MATLAB image processing routines. Walking direction (target-heading angle) was calculated by taking the simultaneous angle between the target position and the participant’s instantaneous direction of locomotion (tangent to the curve) at each point as they travelled through the environment. Since the direction of heading error differed according to the direction of the prism, we flipped the sign on the right prism data so that it could be combined with the left prism data. In line with standard practice, (e.g., Warren et al., 2001) we removed the first metre of the beginning and end of the trajectories from the analysis due to noise. We also excluded any data points that were more than 3 SDs from the mean (defined over observers for the given distance and given trial) or more than 10° from the expected range of 0-8.5°.

2.1.6 *Measurement of perceived direction*

The literature on the coding of allocentric location in rodents indicates that over time, experience of, and attention to, the environment leads to the development of a stable representation of the scene (Frank et al., 2004; Kentros et al. 2004; Monaco et al. 2014). It would be of significant interest if we could find evidence of the development of a representation of allocentric space. Such a development might be revealed by a change in walking trajectory: as the representation became richer, so its contribution to the visual guidance of walking increases and the trajectories straighten. Based on previous work (e.g. Bruggeman & Warren, 2007) we anticipated that trajectories would straighten over trials in our experiment. The problem is that straightening could be due to a different factor, it could result from changes in perceptuo-motor alignment: discrepant optic flow has been shown to shift perceived egocentric direction (via a shift in perceived visual straight-ahead; see Held & Freedman, 1963; Held & Mikaelian, 1964; Herlihey & Rushton, 2012); a change in perceived direction would lead to a change in the curvature of the walking paths (see Rushton & Salvucci, 2001). To address this issue we interleaved measures to track changes in perceptuo-motor alignment. We used two standard measures: Visual straight-ahead (VSA) is a measure of alignment of the eye-head system and proprioceptive straight-ahead (PSA), a measure of alignment in the limb-head system (see Redding & Wallace, 1997, for an overview of measures of perceived direction).

Participants were stood two metres from a wall. Attached to the wall was a ruler with small numbers only visible to the experimenter. We measured VSA by asking participants to verbally indicate when a visual target (a light spot moved by the experimenter along the top of the ruler) was straight-ahead. We measured PSA by asking participants to close their eyes, and position their extended right arm so that it

was pointing straight-ahead. When the participant was confident he or she was pointing to straight-ahead, the participant turned on a laser pointer held in their pointing hand; the experimenter recorded the position of the light spot. The position of the participant was changed at each measurement phase to prevent use of a remembered point on the wall. We measured VSA and PSA five times during the experiment: prior to walking, and after trajectories 6, 12, 24 and 48 (the final trajectory). We combined data for left and rightward prisms by flipping the sign on the right prism data. Changes in perceived direction (VSA and PSA) were calculated by subtracting pre-exposure measures.

2.2. Results

Figure 4a shows the mean target-heading angle over trajectories for each condition. To aid visual comparison, the three conditions (NoMotion, StopGo and Motion) are overlaid and error bars are shown consecutively over conditions, on every third data point. To recap, a target-heading angle less than 8.5° indicates the use of cues other than egocentric direction. In panel B we show the difference between the conditions expressed as t-values.

Figure 4. *a.* Mean target-heading angle across all trajectories. Mean over trial (~ 16.5 m) and observers ($n = 20$ per condition) target-heading angle is shown on the vertical axis. Dashed grey line at 8.5° indicates optical displacement of the prisms. Error bars represent 95% confidence intervals. Solid blue line is NoMotion condition; dashed black line is Motion condition; dotted red line is StopGo condition. Data fit with best-fit (logarithmic) curves. *b.* Differences (t-values), in target-heading angle as a function of trial number. NoMotion-Motion solid line (orange), NoMotion-StopGo dotted line (purple). The dark grey dashed line indicates the t-value for $BF_{10} = 1/3$. Points below the line indicate “substantial” (Kass & Raftery, 1995) evidence the target-heading angle in the NoMotion is not larger than the comparison condition. The light grey dashed line indicates the t-value for $BF_{10} = 3$. Points above the line indicate substantial evidence that the target-heading angle in the NoMotion is significantly larger than the other condition. Test are 1-tailed with predicted order Motion < StopGo < NoMotion.

Visual inspection of Figure 4a reveals that in the key NoMotion condition, target-heading angle was considerably less than the displacement of the prism on every trial (t-tests, all $BF_{10} > 20$; Cohen's $d > 0.80$). Given there was no optic flow in this condition we can interpret this data as providing strong evidence that allocentric location cues can play a key role in the visual guidance of walking.

Next we examined what happens when flow cues are added by comparing the target-heading angle in the NoMotion condition to the Motion (full flow) and StopGo (intermittent flow) conditions. The mean (over trial) target-heading angles are 2.68° (Motion, $SD = 1.21^\circ$), 2.76° (StopGo, $SD = 1.34^\circ$), 2.92° (NoMotion, $SD = 2.14^\circ$). A 1-way, 3-level, Bayesian ANOVA provides “substantial” (Kass & Raftery, 1995) evidence for no difference between the conditions ($BF_{10} = 0.15$; Cohen's $d = 0.063$).

Because mean measures may obscure important differences on specific trials, e.g. on the first trials, we looked at the trial by trial differences. Figure 4b shows the difference, expressed as t-values, in target-heading angle between conditions. Some difference between the NoMotion condition and the other two conditions can be seen over the first 7-8 trials. This suggests that optic flow may have an initial influence but it makes no appreciable difference after a certain distance has been walked.

Previous work (e.g., Bruggeman & Warren, 2010) using enclosed environments demonstrated that target-heading angle changes not only from trial to trial, but also within trajectories. Changes in target-heading angle have been interpreted as indicating the on-line use of optic flow. In Figure 5 we plot the mean target-heading angle as a function of distance walked from the start position. As before, all three

conditions are overlaid and every third error bar is shown; the lower panel shows the differences between the key NoMotion condition and the two comparison conditions expressed as t-values. In line with previous work, the target-heading angle decreases with distance in all conditions (Figure 5a).

Critically, the target-heading angle (Figure 5a) is markedly less than the optical displacement of the prism at all distances in all conditions (all $BF_{10} > 10^5$; Cohen's $d > 1.8$). Figure 5b shows the differences (expressed as a t-statistic) between conditions. Until approximately 13m the trajectories are broadly similar in all three conditions. In the last few metres (see Figure 5a) target-heading angle is lower (and hence trajectories are straighter) when optic flow is present. This suggests an influence of optic flow, though the influence is small - the reduction in target-heading angle is only 10-15% larger when optic flow is present.

Figure 5. a. Mean target-heading error (averaged over trajectories 1-48) between the first metre and the last metre of a trajectory. Mean (over trial and observers) target-heading angle is shown on the vertical axis. Error bars represent 95% confidence intervals. Dashed line at 8.5° indicates optical displacement of the prisms. Solid blue line is NoMotion condition; dashed black line is Motion condition; dotted red line is StopGo condition. **b.** Differences, as a function of distance plotted as a *t*-value, in target-heading angle. NoMotion-Motion solid line (orange), NoMotion-StopGo dotted line (purple). The dark grey dashed line indicates the *t*-value for $BF_{10} = 1/3$. Points below the line indicate substantial/positive evidence the target-heading angle in the NoMotion is not larger than the comparison condition. The light grey dashed line indicates the *t*-value for $BF_{10} = 3$. Points above the line indicate substantial/positive evidence that the target-heading angle in the NoMotion is significantly larger than the other condition. Test are 1-tailed with predicted order Motion < StopGo < NoMotion.

2.2.1. Changes in perceived direction

To recap, we took measures of perceived visual (VSA) and proprioceptive straight-ahead (PSA) so we could factor out their effect on the anticipated (and observed) straightening of trajectories. Figure 6 shows the changes in VSA and PSA. The pattern of PSA changes (Figure 6b) is quite different to the pattern of trajectories (target-heading angle) changes: the PSA changes do not plateau and the order of conditions does not match. The pattern of VSA changes is more similar: VSA (Figure 6a) changed in all conditions, as did the target-heading angle. Changes in VSA also occurred early, similar to the target-heading angle. The only difference is that at the time the first VSA change is measured, the change in the StopGo condition was more similar to the Motion condition than the NoMotion. Given the limited

Figure 6. Mean change in VSA (a) and PSA (b) over time. Phase number (corresponding to trajectories 6, 12, 24 and 48 respectively) is indicated on the horizontal axis, magnitude of realignment is indicated on the vertical axis. Data from the three conditions are overlaid to aid interpretation. Blue diamond markers are NoMotion, black circular markers are Motion condition, red square markers are StopGo. Error bars indicate 95% confidence intervals. Herlihey & Rushton (2010) looked at changes in VSA and PSA after 6 trials. The pattern of VSA and PSA changes over the first 6 trails here is comparable.

number of data points it is not practical to attempt a formal statistical analysis of the similarity between the changes in VSA and the changes over trajectories. However, given the similarities between the trajectory and VSA changes over the 48 trials, it is unwise to interpret the changes in trajectory over trials as having resulted from the development and use of an allocentric representation. It is more parsimonious to assume the changes in trajectory result from a realignment of perceptuo-motor space (specifically perceived VSA).

3. Experiment 2

The key conclusion of Experiment 1 was that allocentric cues provide an important source of information for the online visual guidance of walking to a seen target. To test the robustness of this conclusion we tested whether the results from the key “NoMotion” condition would replicate in a different environment (an interior space with a closer target), where view of the scene was controlled by strobe flashes rather than by the participant, and when the participants were performing a task that precluded them from attending to their walking.

3.1. Methods

3.1.1. Participants

Twelve participants (1 male) took part in the experiment for course credit. All participants had normal or corrected-to-normal vision using contact lenses. The research was carried out in accordance with the Declaration of Helsinki, the study was approved by the School of Psychology Ethics Committee, and informed consent was obtained. The data from Experiment 1, indicated we had sufficient power to justify a large reduction in the number of participants. We decided to reduce to twelve, a somewhat conservative reduction.

3.1.2. Experimental setup

The experimental setup was similar to Experiment 1 but for the following differences:

- The environment was a square room ($8.3\text{m} \times 8.3\text{m} \times 3.4\text{m}$, as such trajectories were much shorter; see figure S2).
- Target posts ($\sim 1.5\text{m}$ high) were placed at two opposite corners of the room.
- Three LED lights (red, yellow and green) were attached to the top of each post. Once per second one of the LED lights flashed briefly (50ms).
- The room was light-tight and during the experiment the room could only be seen when six synchronised ceiling-mounted strobe lights (Equinox Wildzap, 1500W), arranged to evenly illuminate the whole room, were transiently illuminated. Each flash was 5-10ms duration and no after-images were seen.
- Participants wore a helmet with five LEDs so that their position could be tracked by a 16 cameras optical motion tracker (Impulse X2, PhaseSpace Inc., USA).

The advantage of using a strobe is that we can guarantee that no motion cues are present because the flash is so brief. The disadvantage is the briefness of the flash impairs the pickup of allocentric location, it is hard to clearly perceive the sides of the room. To minimise the degradation of allocentric cues we used multiple synchronized strobes to maximise brightness and visibility of the room.

3.1.3. Procedure

The procedure was matched to the NoMotion condition of Experiment 1 but with a few procedural differences. Participants first put on a helmet with trackers and were led to the middle of the room where the trackers were calibrated. After calibration, participants were led, unsighted, back to the starting point. When the participant was ready, the experimenter initiated the trial, and the strobe lights were switched on (flashing for $< 10\text{ms}$ at 1Hz). To ensure participants did not pay undue attention to

the act of walking, they were required to press a button on a remote controller held in their hand every time the red LED flashed. When they reached half a metre from the target post, a beep sound indicated they should stop. The strobe lights, LED lights and notification beep were controlled by a custom program written using Vizard (version 5, WorldViz, Santa Barbara, USA). Each participant walked 5 trials wearing prism glasses. Given that the majority of the changes in trajectory occurred on the earlier trials of Experiment 1, five trials was judged sufficient to reveal any changes.

3.1.4. Measurement of walking trajectories

Head position and orientation were tracked and recorded at 60Hz using a Vizard program. Walking direction was calculated in the same way as in Experiment 1 and the same rules for removal of outliers were applied.

3.2 Results

Figure 7 shows the mean target-heading angle for each trajectory. As in Experiment 1, the target-heading angle was considerably less than the displacement of the prism (8.5°) on every trial (one-sample t-test, all Cohen's $d > 1.11$; all $BF_{10} > 10$) (see Figure 7a). The target-heading angle was also considerably less (one-sample t-test, all Cohen's $d > 0.64$; $BF_{10} > 3$ from 0.6m) than the displacement of the prism from the beginning to the end of the trial (Figure 7b).

Figure 7. a. Mean target-heading angle across all trajectories. Mean over trial (~ 6.5 m) and observers ($n = 12$) target-heading angle is shown on the vertical axis. Dashed line at 8.5° indicates optical displacement of the prisms. Error bars represent 95% confidence intervals. **b.** Mean target-heading error (averaged over trajectories 1-5) between the first half metre and the last metre of a trajectory. Mean (over trial and observers) target-heading angle is shown on the vertical axis. The error bars represent 95% confidence intervals. Dashed line at 8.5° indicates optical displacement of the prisms.

Despite the differences in environment (room vs. outdoors; 7m vs. 17m), access to optic flow information (controlled by the experimenter vs. controlled by the participant), and attentional demands (additional of monitoring task), the pattern of results was similar to Experiment 1.

4. Discussion

The results of Experiment 1 support the hypothesis that when they are salient, allocentric location cues have a role in the online visual guidance of walking to a seen target: the target-heading angle was significantly less than the optical deflection of the prisms (8.5°) in the condition that did not contain optic flow cues (NoMotion). The result of Experiment 2, designed to test this conclusion, using a strobe-illuminated room, provides further support.

Trajectories changed – straightened - over trials. However, the current experiments provide no evidence that the participants, unlike rodents (Frank et al, 2004), developed a stable internal representation of allocentric space from accumulating experience of the environment. It is possible that a build up did occur, but if so we can conclude it must have occurred rapidly, at a rate too fast for us to detect. The most parsimonious explanation for the changes we observed is that the discrepant optic flow realigned perceived visual straight-ahead (see Herlihey & Rushton, 2012).

The trajectories we measured in the Motion condition are comparable to those reported previously by Warren and colleagues, and others (e.g., Warren et al., 2001; Turano et al., 2004). We used a similar enclosed environment (but dissimilar technology) and obtained similar paths. The trajectories are dissimilar to those reported by others (e.g. Rushton et al., 1998; Saunders and Durgin, 2011) who used open environments. This pattern of results across studies is consistent with the conclusion that in open environments egocentric direction is the primary, and often sole, cue, but in enclosed environments, although egocentric cues retain their central role, allocentric location cues have an important part to play.

387

388 It would be premature to suggest that there is no influence of optic flow. In the early
389 trials of Experiment 1, there was a consistent (if not statistically significant)
390 difference between the NoMotion condition and the two conditions that contained
391 optic flow. However, it does not follow that any differences reflect the use of optic
392 flow in the online guidance of walking, they could be due to discrepant optic flow
393 biasing perceived visual straight-ahead (VSA) observed over the same period (see
394 Rushton & Salvucci, 2001).

395

396 **4.1 What allocentric location cues are involved?**

397 In the Introduction, we highlighted allocentric location cues that are based on the
398 perspective projection of the environment boundaries (figure 2). We gave distance
399 cues as an example of other cues that provide information about allocentric location.
400 The literature points to some others. For example, Vishton and Cutting (1995), and
401 later, Hahn, Anderson and Saidpour (2003), found observers were able to judge
402 heading direction from snapshots of an environment presented at intervals of more
403 than two seconds apart when the environment contained distinct objects (e.g., real or
404 wireframe trees). There were few objects in our experiments but the relative
405 movement of those in view could have made a contribution. Macuga, Loomis, Beall,
406 & Kelly (2006) demonstrated that observers were able to judge heading direction in
407 scenes that lack optic flow but do contain stereoscopically defined information about
408 scene layout. The experiments we report were not designed to determine which
409 allocentric location cues were used, but the findings reported here provide a
410 foundation for future work to tease apart different allocentric location cues and
411 determine their role.

412

413 **4.2. Use of other strategies or cues in the current experiment?**

414 Observers can perform “blind walking” –view a scene and then walk blindfolded to a
415 target (Thomson, 1983). If observers used blind-walking technique here, we would
416 expect them to take a straight-line trajectory rather than a curving trajectory that is
417 indicative of the continual online regulation of walking direction. Therefore we can
418 rule out this possibility.

419

420 When a target is close, the drift (change of visual direction) of the object provides
421 information about whether the observer is heading to the left or right of the target
422 (Lewellyn, 1971). No studies have directly examined the use of target drift in
423 walking. One dataset that may demonstrate the utility of target drift is from Harris
424 and Bonas (2002) who found observers walking down a short narrow familiar
425 corridor to an illuminated target while wearing prism glasses, took the same trajectory
426 in the light and dark. One possible explanation of that result is that observers used
427 target drift. In our experiments we removed not only global motion (optic flow) but
428 also object motion (target drift).

429

430 **4.3. Relation to animal literature**

431 The finding that allocentric location cues have a role in the online visual guidance of
432 walking to seen targets highlights a potential link between the different literatures.
433 The findings here suggest that allocentric location cues also have a role in the online
434 guidance of human walking. Neurophysiological work on rodents, and imaging work
435 on humans may provide clues about the neural mechanisms that underpin the

behaviour we observed. Second, based on our results and the broader human literature, we predict a difference in neural coding may be found in animals that are moving through natural open and irregular environments (see also Kupric et al., 2014).

4.4. Combining cues and modelling locomotion

How would allocentric location cues be combined with other cues? Warren et al. (2001) proposed a simple control model based on a combination of optic flow heading and egocentric direction cues, and others have been proposed since (e.g., Wilkie & Wann, 2003; Fajen & Warren, 2007). These models capture behaviour in enclosed environments and could be adapted to accommodate allocentric location cues. An alternative would be to model the behaviour on the assumption that cues are combined to form an internal model of the environment which guides behaviour (Loomis & Beall, 2004).

5. Conclusions

To date, research on the visual guidance of walking to seen targets has focused exclusively on motion cues and egocentric direction cues. The data we report supports the hypothesis that when they are available, as in typical urban enclosed environments, allocentric location cues provide a powerful additional source of information.

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7. Declaration of interest

None.

8. Supplementary materials

The supplementary figures, Fig S1-2 referenced in the paper are to be found at TBA. We also provide additional background information in HerliheySM.doc. Data is available at [TBA]. The analysis code was made available to reviewers, and is available on request.

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478 **10. Author contributions**

479 TH and SKR designed experiment 1, TH collected and analysed the data. DC, SKR
480 and SV designed experiment 2, DC collected and analysed the data. CC wrote the
481 image processing code used in Experiment 1. TH and SKR wrote the original ms,
482 DC, SV and CC contributed to revisions.

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