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Guidance of locomotion on foot uses perceived target location rather than optic flow

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What visual information do we use to guide movement through our environment? Self-movement produces a pattern of motion on the retina, called optic flow. During translation, the direction of movement (locomotor direction) is specified by the point in the flow field from which the motion vectors radiate – the focus of expansion (FoE) [1–3]. If an eye movement is made, however, the FoE no longer specifies locomotor direction [4], but the 'heading' direction can still be judged accurately [5]. Models have been proposed that remove confounding rotational motion due to eye movements by decomposing the retinal flow into its separable translational and rotational components ([6,7] are early examples). An alternative theory is based upon the use of invariants in the retinal flow field [8]. The assumption underpinning all these models (see also [9–11]), and associated psychophysical [5,12,13] and neurophysiological studies [14–16], is that locomotive heading is guided by optic flow. In this paper we challenge that assumption for the control of direction of locomotion on foot. Here we have explored the role of perceived location by recording the walking trajectories of people wearing displacing prism glasses. The results suggest that perceived location, rather than optic or retinal flow, is the predominant cue that guides locomotion on foot.

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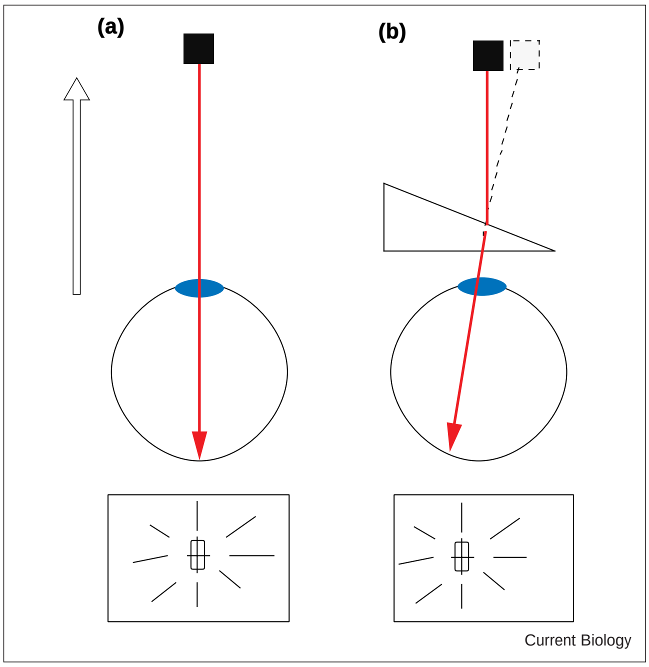
Results and discussion

We start with an informal observation. W.V. has unilateral visual neglect (UVN). His wife reported to us that he consistently walks a peculiar veering course to objects of interest [17]. Current theories of perception of locomotor direction based on optic flow seem unable to explain or predict W.V.'s trajectory. However, UVN is associated with the misperception of location. We were perplexed with the report of W.V.'s behaviour and so attempted to manipulate the perceived target location for normal individuals, to see if similar veering trajectories could be induced.

Flow-based theories of heading are concerned with the perception of locomotor direction relative to objects or elements in the environment or image. In the simplest case, for an eye fixed in its socket, the locomotor direction is specified by the position of the FoE within the image, for example, 5 degrees to the left of a target object. When a horizontal wedge prism is placed before the fixed eye, the entire image of the world is shifted on the retina (Figure 1). Because the whole image is deflected by a

Figure 1



Retinal position of an object located straight ahead of the participant (a) without a prism and (b) with a prism. Lower panels show the instantaneous optic flow field corresponding to translation directly towards the target (in the direction indicated by the open arrow) without and with a prism. The FoE is coincident with the target, but in (b) both the target and the FoE are displaced to one side. If the relative position of the FoE and the target is used to control locomotion on foot then the participant should walk directly towards the target. Changing to egocentric coordinates and hypothesising that independent neural systems are responsible for determining the position of the FoE and the target does not change the prediction. Such a model would predict a prism-induced error in both the coordinates of the FoE and the coordinates of the target. This constant error would cancel out, leaving the correct relative position of the FoE with respect to the target.

prism, the position of the FoE relative to the target and all other objects within the image or environment is unchanged. The perception of locomotor direction should remain veridical (in the above example, still 5 degrees to the left of the target) if perception of locomotor direction relies upon optic flow (this is also the case when locomotor direction is recovered from a more complicated flow field including an eye movement). For example, a simple and representative flow-field-based strategy for reaching a target ('FoE–target' strategy) can be described as follows: first, walk forward; second, locate the target within the image; third, locate the FoE from the flow within the image; and fourth, if the target and FoE are not coincident, then modify the locomotor direction and reiterate the loop. With or without prisms the FoE–target strategy (and all other flow-based strategies, see Figure 1 legend) should result in a straight course to a target.

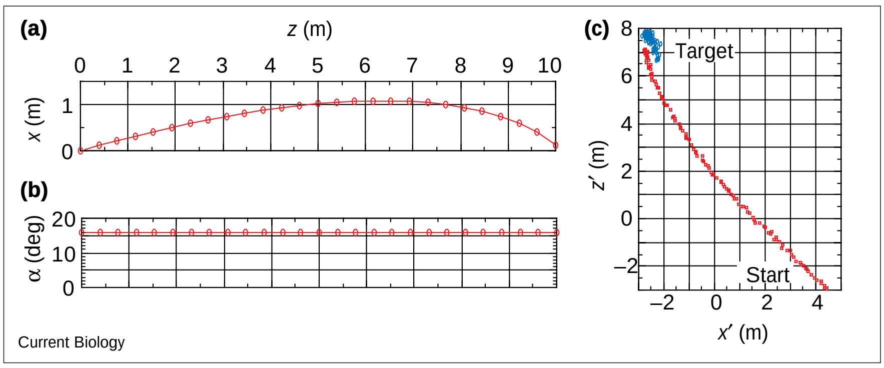
A prism, however, changes the perceived egocentric location of an object relative to the midline of the body (the locomotor axis) [18]. If perceived location guides locomotion on foot, then placing prisms in front of the eyes should perturb perception and control of locomotor direction. For example, a simple strategy based upon perceived location ('perceived-direction' strategy) can be described as follows: first, walk forward; second, rotate the gaze to fixate the target; third, rotate the body in a direction that should reduce the angle between the gaze and the midline; and fourth, evaluate the difference between the angle of the gaze and the orientation of the body and reiterate the loop. Under normal circumstances the perceived-direction strategy will work successfully and result in a straight course to the target. If the person consistently misperceives the location of an object relative to their body (as happens when wearing prisms), or misperceives the midline of their body (as often happens after brain injury), then they will misalign their locomotor axis with the true direction of the target and produce a constant heading error. Thus, a person wearing prisms and using this strategy should walk a veering trajectory (Figure 2).

We set out to examine the respective influence of the flow field and perceived location in guiding locomotion. Participants wore glasses with wedge prisms or Fresnel prisms deflecting right or left. An experimenter held out a target ball and asked the participants to walk over and touch the ball. Participants walked at a brisk pace for approximately 10 to 15 metres and their trajectories were recorded by a camera 33 metres overhead. Video frames were captured on a PowerMac 8500 computer and digitised using the public domain NIH Image software [19].

The trajectories taken by the participants followed a curved path similar to the perceived-direction prediction. From the digitised data it was possible to determine the locomotor direction at any point during the trajectory (tangent to the curve of their path), the direction of the target, and the difference between them, defined as the target–locomotor direction error (α). The simple perceived-direction strategy predicts that α should be equal to the angular deflection of the prism. Figure 3 shows the values of α as the trial progressed. In general, α was close to the prism deflection angle, as predicted by the perceived-direction model, and clearly not close to zero, as a flow-based model would predict.

Three issues arise in the interpretation of this initial result. First, prisms occlude a small, highly eccentric, part of the visual field on one side and increase the field slightly on the other. In bees, locomotor direction is controlled by equalising the amount of flow in the two halves of the visual field [20]. If flow was summed over the whole of the left and the whole of the right hemifields, then a crude equalisation strategy could be slightly perturbed by

Figure 2



(a) Simulation of the trajectory when wearing prisms that is generated by a simple model using target direction rather than optic flow. The *x* and *z* are distances parallel and perpendicular, respectively, to the starting position of the participant (facing along the *z* axis). A plan view shows the predicted trajectory of a prism-wearing participant walking in the perceived direction of the object (the perceived direction is offset from the actual position by the angular deflection of the prism glasses). The plot is for a 16 degree deflection, the approximate angular deflection of the wedge prisms used in our experiments. (b) Target–locomotor direction error, α, between the instantaneous direction of the target and the direction of locomotion (the tangent to the curve) which remains constant throughout the trajectory. (c) A representative trajectory (participant 3, wedge prism, going right in Figure 3) of an observer (shown in red) approaching a target (blue). The plot shows raw digitised data, with axes *x*′ and *z*′ showing distances in camera coordinates.

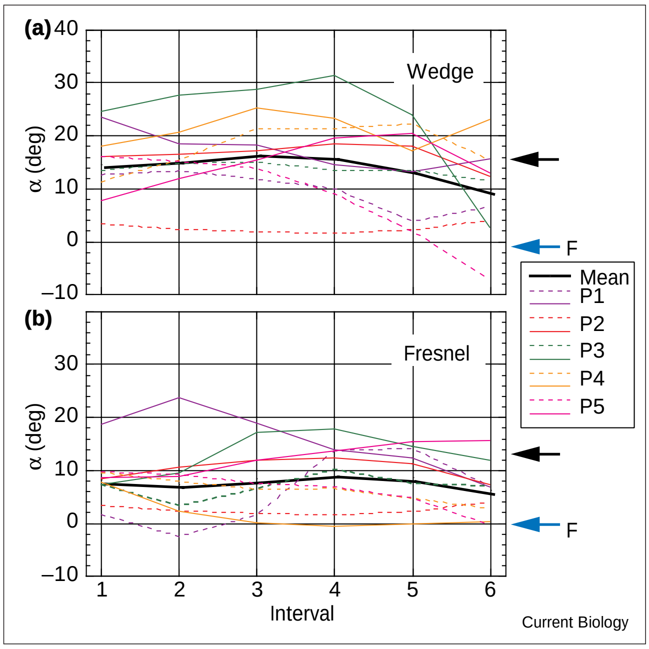
wearing prisms. There is recent evidence that humans can use an equalisation cue, but the influence of the cue is readily attenuated by other flow information such as the FoE [21]. Thus, it appears very unlikely that use of such a strategy could explain our results.

Second, in contrast to most studies of perception of locomotor direction, participants moved by natural walking through a natural environment. However, our study inevitably introduced some 'cue-conflict'. Are there grounds for suspecting that participants abandoned normal control strategies and behaved differently because they noticed the effects of the prisms? We believe not, because the conflict was small, all flow-based information remained congruent and veridical, and the prisms perturbed only perceived location, a previously unrecognised cue. Also, participants did not appear to have problems: they walked at a brisk pace, showed no hesitancy and little awareness of their peculiar trajectory. This behaviour can be contrasted against the conflict associated with trying to consciously override the influence of prisms: in an informal replication of our study (Brian Rogers, personal communication), participants tried explicitly to use motion parallax (the relative motion between objects in the environment) to guide themselves. This was partially successful, but it was noted that 'the feet keep trying to do something different'. These observations concur with our own: it feels unnatural to use such a deliberate motion-parallax strategy and a participant trying to do so can be easily identified by their odd gait with their body twisted at the waist. In summary, problems relating to cue conflict and unnaturalness of the task or visual environment were minor in this study.

Third, it could be hypothesised that flow is used in our task, but that some time is required before it can be used. If so, participants might have started on the wrong trajectory and then needed several seconds to perceive and act on the flow. Such periodic regulation of heading would predict a non-straight trajectory, but a late correction to the trajectory would show up as a dramatic reduction of α at some time during the time course. Specifically, α should reduce to zero after a second or so (about 1/7th of the way along the trajectory). This is clearly not the case as even the longest estimate of a locomotor reaction-response time [7] would predict that locomotor direction would be corrected before half the trial distance is walked. Nonetheless, we thought it informative to test whether locomotor direction was continuously rather than periodically regulated.

In a second study we moved the target into or away from the path of the participant. For the perceived-direction model, if locomotor direction is continuously controlled the prediction is the same as that for a stationary target: that α retains an approximately constant value throughout the trial (see Figure 4 legend for qualitative predictions). The path will be clearly dissimilar from a predicted

Figure 3

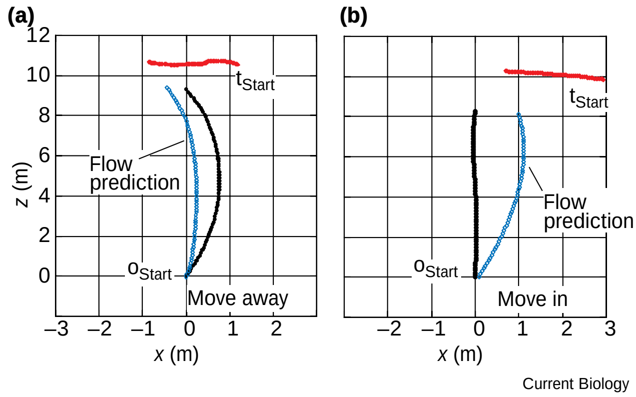


Mean target–locomotor direction error (α) across the trial for five participants. Raw trajectory data were smoothed with a gaussian curve, σ = 8 data points (1/3 sec), window = 16 data points (2/3 sec); smoothing removes the first and last 16 data points. Trials were normalised and divided into six intervals (by distance; mean total distance = 12.7 m, standard deviation = 1.3). **(a)** The error α when participants P1–P5 wore wedge prisms (~16 degree angular deflection), and **(b)** when they wore Fresnel prisms (~14 degree deflection; wider field of view, lower optical quality). Full lines indicate a left deflection and dotted lines, a right deflection. The thick black line on each plot shows the mean across all participants and both deflection directions. Black arrows show the prism deflection (perceived-direction prediction) and blue arrows the FoE–target prediction. In general, the error, α, was fairly constant across the whole trial for both types of prism. For the wedge prisms, α was close to the value of the prism deflection (black arrow). Fresnel prisms produced proportionately less veering than wedge prisms. Fresnel prisms have a wider field of view and we hypothesise that this may be important, not because more peripheral flow can be seen but rather because parts of the body, in particular the nose, are visible [24] and this may serve to attenuate the effect of the prisms on misperception of egocentric directions.

FoE–target trajectory. Results were similar to those for the previous static target set. The value of α was found to remain approximately constant throughout the trial (Figure 4 shows a plan view of two trials), as predicted by the perceived-direction model. Thus, direction of locomotion is controlled on-line, in a continuous manner. These data discount a possible flow latency hypothesis.

It is parsimonious to conclude that when moving on foot a person's trajectory is predominantly controlled by the perceived location of a target relative to the body. This is an efficient and economical solution, as knowledge of the orientation of the body with respect to objects is necessary anyway during interception or passing.

Figure 4



Two representative smoothed trajectories of a prism-wearing participant approaching a moving target (note the difference in scaling of horizontal and vertical axes). The red line indicates the trajectory of the target, the black line the trajectory of the participant. The blue line indicates the predicted trajectory that would result from using flow and walking in the instantaneous direction of the target. It is clear that participants do not follow trajectories that would be predicted from using flow. **(a)** The participant initially walks to the right of the target and the target starts to move left, away from the participant's path. **(b)** The participant initially walks to the left of the target and the target moves left, into the participant's path. Both the predicted direction and flow plots shown assumed that observers do not anticipate the future position of the target and walk towards that point. From our raw data (not shown) it does not appear that observers anticipate the position of the target. For the 'move in' condition, observers maintained an approximately constant α, at the prism-deflection value, which we would not expect if they had anticipated the future position of the target and moved accordingly. Calculation of α shows that it remains approximately constant throughout the trial (mean of first interval = 11.6 degrees, mean of last interval = 11.2 degrees). This is similar to the results when using a stationary target and compatible with the use of a perceived-direction strategy and continuous regulation of direction of locomotion.

We note that many studies have required judgements of locomotor direction after 1–2 seconds of viewing a simulated translation through a projected abstract environment [5,12,13]. These experiments have shown that humans can determine their direction of locomotion from a flow field. Therefore, it appears likely that humans will exploit this information in some situations. Our study reveals, however, that a person walking through a real environment appears to be primarily influenced by perceived location, not optic flow (see Llewellyn [22] for a similar conclusion based upon target drift).

To return to W.V., do these results help us to account for his veering walks? We believe they may. It has been reported that some patients with UVN misperceive their midline [23]. If W.V. perceives his midline as deflected from its true position, then when he places the target apparently 'straight-ahead' and walks forward, he will not be walking towards the target. Therefore, we would predict a similar shape of trajectory to that shown by normal individuals wearing prism glasses. The possibility also arises that the veering of an individual with UVN may be nulled through the use of prism glasses. We must wait for another suitable patient to test this model of UVN veering as, fortunately, W.V. has learnt to walk in a straight line. Interestingly he now walks in a straight line even when wearing prisms — perhaps he has learnt to determine locomotor direction from the flow field.

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