Going against the flow

In a recent review that brings together psychophysics, neurophysiology and computational modelling, Lappe *et al.* provided an interesting and comprehensive account of how visual motion, specifically 'optic flow', may be used to perceive and guide human locomotion[1]. The review presented compelling evidence that the brain contains the appropriate neurones, and that humans possess the appropriate sensitivity, for optic flow to be useful for navigation. A critical issue, briefly touched on in the review (in Box 3, p. 334) is whether the fact that optic flow is available to humans necessarily means that it is the primary cue for navigation in the natural environment. Lappe *et al.* also described how non-flow information could be used in the control of locomotion, but the issue of how these other cues combine with optic flow was considered an outstanding question. In this letter we would like to highlight some recent research that questions whether optic flow information is indeed the dominant information source during human locomotion.

As Lappe *et al.* suggest, it is indeed difficult to walk with the eyes closed, but it is not difficult to walk in situations where optic flow is absent or minimal; for example, at night, when very little optic flow information is available, or during snowstorms, when optic flow information might simply be wrong. It is clear that optic flow cannot be used in such situations and that other sources of information must be used for navigation. However, if we can walk without optic flow, do we also use other information when flow *is* available? Most of the optic flow literature does not address this question, because the paradigms that are used are designed to isolate optic flow, and do not include other visual information that would be present in the real world. However, one recent study has directly tested the assumption that optic flow is the dominant source of visual information in human locomotion by pitting optic flow against a different cue – visual direction – in a natural walking task in the real world[2].

To use visual direction as a cue for navigation requires the observer to monitor the angular direction of the target relative to their own body. The simplest strategy is to keep the target 'straight ahead'[3]. If the target drifts off to one side, the observer should take corrective action by turning to re-align their body towards the target. In the real world, optic flow and visual direction strategies are mutually redundant, since either source of information allows you to reach your target[4]. However, when displacing prisms are placed over the eyes during locomotion the information provided by optic flow and direction-based strategies can be dissociated. When a displacing prism is placed before the eyes the image of the world is shifted on the retina by an amount corresponding to the power of the prism (see Fig. 1A). The result is that objects that appear to be straight ahead when viewed through the prisms, are actually positioned to one side. Rushton *et al.* described a simple model that predicts that if observers use the visual-direction strategy while wearing prisms they will attempt to walk directly towards the target, but will actually transcribe a curved path[2] (Fig. 1B). This is because each step towards the perceived (but incorrect) direction of the target will need to be followed by a re-alignment of the body towards the perceived (but still incorrect) target position prior to the next step. However, displacing prisms do not change the differential properties of the flow field such as the focus of expansion, so the focus of expansion will still coincide with the perceived target direction. Thus, flow-based locomotion strategies should be unaffected by prisms.

In the critical experiment, Rushton *et al.* showed that the prediction of the model was upheld: observers wearing prisms that deflect by 14 or 16 degrees transcribe a curved trajectory when attempting to walk towards a target. This suggests that when both sources of information are available the visual-direction strategy is dominant This simple regulation-of-direction strategy is powerful because it relies on target position and is therefore not affected by the motion or 3-D structure of other objects in the environment. For example, it can account for interception with moving targets[2], and would also be able, in theory, to account for path following and navigation in the presence of moving objects, without elaboration or modification.

But such cue-conflict paradigms are always problematic, as they seldom occur in the real world. How can we test whether direction is the only information used, or whether it is the dominant cue, along with other cues including flow, which also contribute? It has been demonstrated that, with effort, cues including flow, local motion parallax and ground markings can be used to consciously over-ride visual direction[5,6]. However, these tasks involve deliberate conscious use of cognitive strategies that cannot fully over-ride the direction information. That these strategies are inappropriate in the natural environment can be illustrated by showing how easily they can be disrupted. If observers are given a secondary task (e.g. visual counting), they instantly revert to the visual-direction strategy (S.K. Rushton, pers. commun.). Research with a different emphasis provides stronger evidence that direction alone is used. If direction were the only cue, we would predict that behaviour should be unaffected by whether optic flow information is conflicting or congruent in a given situation. This is in fact the case: similar curved paths are produced in the dark (with only a single target light visible) where no flow is present, and in the light, where flow and direction information conflict[7]. If flow were used in conjunction with direction, we would expect some modification in full lighting conditions, but this was not found.

These results are consistent with optic flow not being used at all to guide direction during human locomotion on foot. It is fashionable to assume that multiple cues are combined for any percept, because of the richness of available information for an observer to use. However, we have yet to see strong evidence that there is a role for other cues such as flow in the control of locomotion direction. We challenge flow researchers to provide some compelling evidence for a significant role for optic flow in the control of the direction of locomotion on foot. The challenge that remains for those of us who presume direction to be the sole source of information for the control of locomotion is two-fold. First, to produce a complete model of locomotion on foot, and second, to account for the use of the extensively documented human sensitivity to optic flow.

We can tentatively point to several situations where flow might be useful and for which sensitivity to it might have evolved. Optic flow is potentially useful for the essential task of assessing the speed of one's locomotion, which we have not addressed here. This, in turn, could be helpful in the regulation of gait and perhaps in more cognitive aspects of navigation, such as memorizing and learning routes. Furthermore, optic flow might be involved in the control of posture and in the perception of vection, where purely visual information can result in a feeling of moving forwards.

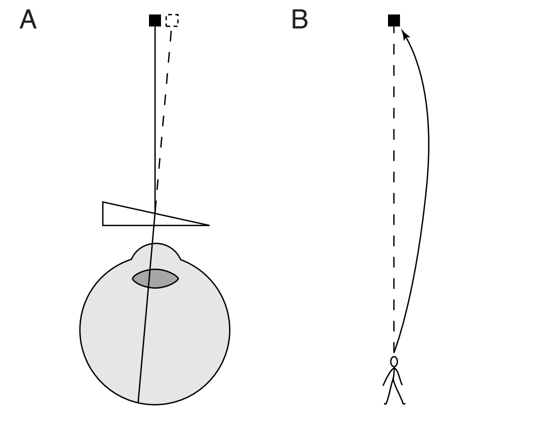

Fig. 1. Locomotion while viewing through a prism. (A) With a prism held in front of the eye, the retinal image of an object located straight ahead (dark square) will be deflected to one side (solid line indicates light path). The apparent location of the object will thus be displaced (dotted line and square). **(B)** If visual direction guides locomotion, the observer will walk in a curved trajectory (solid line) when viewing through prisms, rather than the straight path predicted by the use of flow (dotted line). Curved trajectories have been found experimentally[2] (trajectory shown here is hypothetical).

We believe that it would now be fruitful to reconsider the use of optic flow and to design tests to explore its use for purposes other than simple control of locomotion direction.

Julie M. Harris
Department of Psychology, University of Newcastle, UK.
tel: +44 191 222 8815
fax: +44 191 222 5622
e-mail: j.harris@ncl.ac.uk

Brian J. Rogers
Department of Experimental Psychology, University of Oxford, UK.
tel: +44 1865 271322
fax: +44 1865 310447
e-mail: brian.regers@psy.ox.ac.uk

References

1 Lappe, M. *et al.* (1999) Perception of self-motion from visual flow *Trends Cognit. Sci.* 3, 329–336
2 Rushton, S.K. *et al*. (1998) Guidance of locomotion on foot uses perceived target location rather than optic flow *Curr. Biol.* 8, 1191–1194
3 Llewellyn K.R. (1971) Visual guidance of locomotion *J. Exp. Psychol*. 91, 245–261
4 Warren, W.H. (1998) Visually controlled locomotion: 40 years later *Ecol. Psychol.* 10, 177–219
5 Rogers, B.J. and Allison, R.S. (1999) When do we use optic flow and when do we use perceived direction to control locomotion? *Perception* 28, S2
6 Warren, W. and Kay, B.A. (1999) Control of walking from optic flow *Perception*,28, S1
7 Rogers, B.J. and Dalton, C. (1999) The role of (i) perceived direction and (ii) optic flow in the control of locomotion and for estimating the point of impact *Invest Ophthalmol. Visual Sci.* 40, S764

Reply to Harris and Rogers

Harris and Rogers argue that research on visual flow for navigation is interesting but irrelevant for the guidance of locomotion [Harris, J.M. and Rogers, B.J. (1999) Going against the flow *Trends Cognit. Sci.* 3, 449–450][1]. They base their arguments on findings that suggest that the use of visual direction *per se* rather than the structure of the visual flow is required for proficient walking.

In support of their assertions they cite a study in which subjects wearing about 15° prisms could not walk straight towards a visual target[2]. Instead they follow a curved path that bulges outward in the direction of the visual displacement by the prism. This condition, the authors claim, pits the direction strategy against the flow based strategy for visual navigation. In line with the observations, the ego-centric direction based strategy would predict a curved path towards the target when wearing prisms. The flow based strategy, however, would enable a straight walk toward the target, as it would entail corrective movement only when the focus of expanding (FOE) is not aligned with the goal for the walk. Because the prism displaces the entire image it will not displace the FOE relative to the target and adjustments of the walking direction will not be specified by the flow. This is true, but does not necessarily lead to the conclusion that a prism should have no effect whatsoever on the walking direction if one attempts to align the FOE and the target.

Does the representation of the flow based strategy by Rushton *et al*. and Harris and Rogers stand to reason? The argument supposes that the flow based strategy guides steering (walking) using differential signals. The misalignment of the FOE and the target evokes corrective movement, but the actual direction of the FOE is irrelevant for steering. If our bodies were spherical and had means of isotropic propulsion an FOE strategy as proposed by Rushton and colleagues (and Gibson for that matter) could work. But our body is not. Moving in a straight line perpendicular to our hips requires the use of a different walking pattern than walking parallel to our hips. *Ipso facto*; this applies to changes in locomotor direction. Thus, although the alignment of the FOE with a target will enable one to move towards a target, it is by no means sufficient information to specify the particular walking direction required. To do so all visual (including retinally based FOE direction) information must be transformed to the body centric frame and this involves a transformation of visual direction that *is* affected by the prism. Moreover, while the prism does not influence the alignment of FOE and target it will induce large asymmetrical distortions of the peripheral flow pattern and hence influence any flow based strategy that uses not only the FOE but the entire structure of the flow. Thus, a more realistic visual flow based strategy of navigation would predict outcomes no different from the direction strategy.

To walk towards a goal one must control the walking direction during the movement but also at the start. Obviously, before subjects begin to walk optic flow is not available, and so the initial information for the starting direction can only come from the perceived direction of the goal. Thus, initial walking direction must be influenced by prisms irrespective of whether optic flow is used during walking or not. The source of information that is used to correct the initial mistake (target direction or visual flow) can only influence the shape of the trajectory at a later time. Warren and Kay analysed the trajectories of walking experiments in a virtual reality environment, and their results provide clear evidence for the usage of flow in this context[3].

The target-direction based strategy may appear more simple, than the flow based strategy. But invoking parsimony as a deciding principle for brain theories is tricky, given the brain's complexity and that of the tasks it has evolved to perform. For example, one important asset of using flow is that the information for the goal of our movement is distributed over the entire visual field. Thus, if the target we are walking to is temporarily occluded by a passing object or by an obstacle that we need to circumvent, the flow still specifies heading and thus can help us to maintain course. It is known that objects crossing our path have only a marginal effect on the perceived heading direction[4,5]. Moreover, an environment in which individual objects are difficult to recognize or track over time (like walking through dense undergrowth in a forest) may complicate visual navigation based on the direction to a target more than navigation based on the direction of the FOE relative to the body.

In conclusion, we agree that adjusting our actions on the basis of the nonalignment between the FOE and a visual target is not the major visual strategy for walking towards a target (although it might be preliminary to discount it completely given the results in Ref. 3), but we disagree with Harris and Rogers that this questions the use of flow for visual navigation altogether. The visual flow informs our brain about our current direction of motion in the retinal frame. The transformation to the bodycentric frame is required to guide our walking movement and it is this transformation that needs to be recalibrated when wearing prisms. Less parsimonious as this explanation may seem, the FOE provides a token for the ego-motion direction that is distributed over the entire visual field, thereby providing information that is robust to occlusion, noise and potential confusion of similar targets. It is the robustness of the information in the flow that tempts us to prefer the less parsimonious explanation for visual navigation or 'to prefer Ockham's beard over his razor' as Ramachandran put it once so eloquently.

Markus Lappe, F. Bremmer and A.V. van ben Berg
Department of Zoology and Neurobiology, Ruhr-University Bochum, 44780 Bochum, Germany
tel: +49 234 322 4350
fax: + 49 234 321 4278
e-mail: lappe@neurobiologie.ruhr-uni-bochum.de

References

1 Harris, J.M. and Rogers, B.J. (1999) Going against the flow *Trends Cognit. Sci.* 3, 449–450
2 Rushton, S. *et al*. (1998) Guidance of locomotion on foot uses perceived target location rather than optic flow *Curr. Biol.* 8, 1191–1194
3 Warren, W.H. and Kay, B.A. (1999) Control of walking from optic flow *Perception* 28 (Suppl.), 1
4 Warren, W.H. and Saunders, J.A. (1995) Perceiving heading in the presence of moving objects *Perception* 24, 315–331
5 Royden, C.S. and Hildreth, E.C. (1996) Human heading judgments in the presence of moving objects *Percept. Psychophys.* 58, 836–865