Heading detection from optic flow

SIR — The question of whether humans can visually detect the direction of egomotion in the presence of a simulated eye rotation has been the subject of recent debate[1-3]. Psychophysical studies using slightly different stimulation procedures have yielded very different results when eye rotations in excess of 1 degree s^{-1} were simulated. But the flow stimuli used in these studies do reveal a qualitatively different pattern of motion when the flow actually arriving on the retina is analysed (Fig. 1). In situations where humans succeed[1,3], the retinal flow field is overall centrifugal in structure, whereas in situations where humans cannot correctly detect their direction of heading[2], it is not.

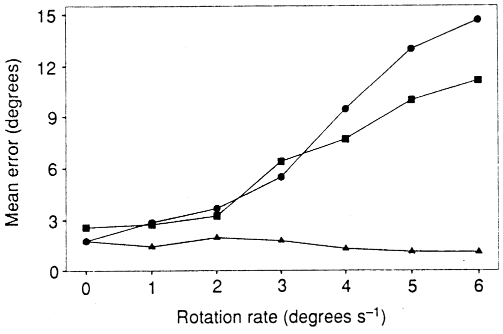

FIG. 2 Mean errors yielded by a network model of heading detection for different flow field stimuli and varying amounts of rotation. When the eye rotation is due to the fixation of a ground plane element, as in Fig. 1*b*, the heading error is low and independent of rotation rate (triangles). When eye rotation around a vertical axis is superimposed, as in Fig. 1*c*, the error rises drastically as the rotation rate increases (circles). The same is true when instead of a ground plane the observer moves through a random cloud of dots at a speed of 0.5 m s^{-1} (squares). In this case, too, the retinal flow field is not radial but rather lamellar for higher rotation rates. Visual field diameter was 34°, and observer speed in the first two simulations was 1.9 m s^{-1}. The network model is a biologically plausible implementation of a least-square algorithm for heading detection[6]. In the input stage of the network the retinal flow is encoded by a population of direction-selective motion detectors which are modelled after cells in visual cortical areas PMLS in cat or MT in monkey. The population contains an anisotropy such that the preferred directions of the motion detectors are arranged in a centrifugal or circular fashion around the fovea, and no centripetal preferences are present. The outputs of the motion detectors feed into a second stage in which the direction of heading is recovered. Cells in this layer form populations that test the compatibility of the measured retinal flow field with a specific preferred heading direction. The best matching direction can finally be detected by a simple winner-take-all scheme, or another more elaborate design which operates on the population activities.

It has been found independently in the visual cortex of cats and monkeys that most cells in some areas specialized for motion processing favour movements away from the fovea or area centralis[4,5]. This centrifugal bias is present in cortical areas PMLS (cat) and MT (monkey), and has been hypothetically linked to the processing of optic flow fields during egomotion.

To see whether such an anisotropic distribution of motion detectors could be related to the differences observed in human psychophysics, we introduced a similar anisotropy in a proposed network model of heading detection. The model uses motion detectors similar to cells in PMLS and MT to encode the retinal flow field and in a second stage recovers the direction of heading with populations of cells designed to implement a least-square heading detection scheme. In computer simulations, our model cells respond to various combinations of expanding, contracting, rotating or translating random-dot patterns[6]. Interestingly, similar response properties have been described for a subclass of cells in monkey visual area MSTd, which is a stage of the visual motion pathway in monkey cortex subsequent to area MT[7-10].

When we established an anisotropic distribution of direction preferences in the network's input layer by removing all cells with preferred direction towards the fovea, the network exhibited differences in detecting the direction of heading from different flow field stimuli which were similar to those in humans (Fig. 2). This suggests (1) that the observed differences in humans could be related to a specialization of the heading detection system to centrifugal flow fields; and (2) that an anisotropic distribution of motion detectors seems to be a reasonable design for ground-living mammals, for which the fixation of a stationary object somewhere near the movement trajectory is probably the most common condition of egomotion.

Nevertheless, accurate heading detection might also be of vital importance when a moving target is tracked instead of a stationary object. The experiments of Royden *et al.*[2] indicate that this is a more difficult task, and we might not be able to perform it had we not the benefit of extraretinal information about our eye

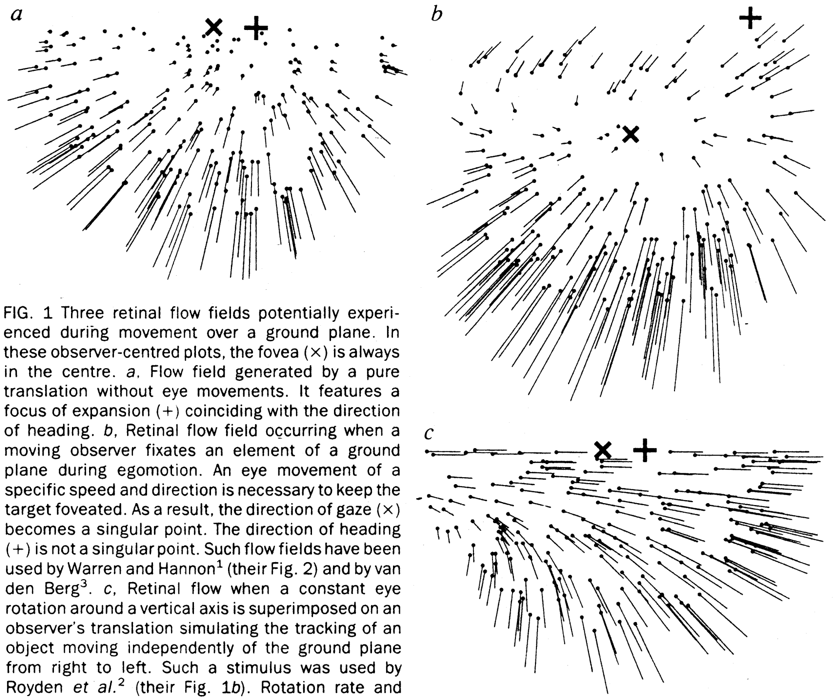

FIG. 1 Three retinal flow fields potentially experienced during movement over a ground plane. In these observer-centred plots, the fovea (×) is always in the centre. *a*, Flow field generated by a pure translation without eye movements. It features a focus of expansion (+) coinciding with the direction of heading. *b*, Retinal flow field occurring when a moving observer fixates an element of a ground plane during egomotion. An eye movement of a specific speed and direction is necessary to keep the target foveated. As a result, the direction of gaze (×) becomes a singular point. The direction of heading (+) is not a singular point. Such flow fields have been used by Warren and Hannon[1] (their Fig. 2) and by van den Berg[3]. *c*, Retinal flow when a constant eye rotation around a vertical axis is superimposed on an observer's translation simulating the tracking of an object moving independently of the ground plane from right to left. Such a stimulus was used by Royden *et al.*[2] (their Fig. 1*b*). Rotation rate and translation speed in *c* are identical to *b*, only the direction of the eye movement differs. As in *b*, the direction of heading (+) is not a singular point. The overall structure of the flow field in *c*, however, is quite different from the one in *a* and *b*. In *c*, the individual movement vectors are arranged in a curved fashion, suggesting a movement along a curved path, whereas in *a* and *b* the flow fields have an overall centrifugal structure. Visual heading detection in humans works well with stimuli as in *a* and *b* (ref. 1, 3), but fails with flow fields of type *c* (ref. 2).

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movements. Undoubtedly, extraretinal information is used by the human heading detection system to make otherwise unsolvable tasks less ambiguous, as has been previously demonstrated for movements towards a vertical plane[1]. We do not intend to suggest that humans (or animals in general) do not use extraretinal information; our main interest is rather the possible adaptation of the visual system to frequently experienced natural flow fields in the sense of Gibson's 'visual ecology'[11].

Markus Lappe
Departments of Zoology
and Neurobiology,
Ruhr University Bochum,
Bochum,
D-44780 Germany
Josef P. Rauschecker
Laboratory of Neurophysiology,
NIMH,
Poolesville,
Maryland 20837, USA