Radial optic flow induces vergence eye movements with ultra-short latencies

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An observer moving forwards through the environment experiences a radial pattern of image motion on each retina. Such patterns of optic flow are a potential source of information about the observer's rate of progress1, direction of heading2 and time to reach objects that lie ahead3. As the viewing distance increases the time to reach objects that lie ahead, the observer must continuously adjust the vergence angle between the eyes. The primary visual cue used to control convergence is binocular disparity4, though changes in object size5 as well as static perspective and overlap cues6 can also be used. It occurred to us that optic flow might also make a contribution as it charts the observer's rate of forward progress.

Our experimental subjects faced a vertical screen onto which large random-dot patterns were back-projected. Steps of radial flow, achieved by switching between two projected images signalling radial displacement and a size change, were applied 50 ms after the subject's eyes fixated the centre of the screen. The flow patterns elicited pure horizontal vergence (negligible vertical Vergence) at latencies of roughly 80 ms in the four subjects tested. As expected from the geometry, centrifugal flow (signalling approach) resulted in increased convergence whereas centripetal flow (signalling retreat) resulted in decreased convergence. Sample vergence velocity profiles, obtained with centrifugal steps of various amplitudes (expressed in terms of the percentage change in apparent viewing distance), are shown for one subject in Fig. 1b. Initial responses were quantified by measuring the change in vergence over a 33–ms period commencing a fixed time (95 ms) after the onset of the stimulus. This meant that our measures were restricted to the initial (open-loop) vergence responses that were generated by the radial flow before it had been affected by eye-movement feedback. These measures are plotted against the percentage change in apparent viewing distance in Fig. 1c, for both centrifugal and centripetal flow. For a given step size, the increases in convergence with centrifugal flow were always larger than the decreases with centripetal flow (compare with ref. 10). Optimal steps changed the apparent viewing distance by 2–4%.

Vergence velocity profiles were always transient, rising to a peak in 30–50 ms and then declining. In our artificial viewing situation, the vergence responses to radial flow would result in binocular disparity, which would in turn tend to generate vergence in the opposing direction. However, disparity-induced vergence has been shown to have a latency approximating that of the radial-flow vergence11, indicating that its earliest effects could not occur until about 80 ms after response onset. The transient nature of the radial-flow vergence cannot therefore be due to the ‘closing of the disparity-vergence loop’. This conclusion is also supported by the finding that initial vergence responses were still transient with monocular viewing (discussed later).

When an observer moves forwards, retinal images not only undergo centrifugal motion but also get larger (Fig. 2a), as was the case in the above experiments. Changes in the size of a small foveated target have been shown to elicit weak vergence eye movements in humans, but at latencies estimated to be in excess of 200 ms (refs. 7, 8). In our case, using large multi-element patterns and shorter time intervals, the size changes were irrelevant, and eliminating the size cue (as in Fig. 2b) had little effect on the vergence responses. Vergence responses to radial flow alone were almost the same as those to radial flow plus size change, and pure changes in size (as in Fig. 2c) failed to generate significant vergence (Fig. 2d).

We propose that these vergence eye movements represent a binocular response to the radial pattern of flow. However, an alternative explanation might be that tracking is essentially monocular, each eye tracking only the motion that it sees and with a strong preference for motion in the nasal hemifields. In this case, with centrifugal flow there would be a net motion vector towards...
the nose in the nasal hemifields and each eye would independently track that motion, the result being increased convergence. With centripetal flow there would be a net motion vector away from the nose in the nasal hemifields and individual eye tracking would result in decreased convergence. Masking different parts of the flow fields seen by each eye shows that this is not the correct explanation (Fig. 3). When one eye was covered, both eyes still converged, albeit more weakly. Further, the convergence persisted when both nasal hemifields were masked off. Here each eye moved in the opposite direction to the net motion vector that it saw. For example, the right eye saw net motion to the right and yet moved to the left. The convergence even persisted when the subject’s view was restricted to only one temporal hemifield. The latter result is particularly revealing about the sensing mechanism that decodes the flow pattern. Despite there being a clear net motion vector to the right, the system still responded correctly, as though compensating for forwards (rather than leftwards) motion, hence the convergent (rather than conjugate rightwards) response. Presumably, the (opposed) vertical components of the flow pattern are critical here for the system to draw this distinction between radial flow (signalling forwards and backwards motion) and planar flow (signalling side-to-side motion). We obtained very similar data when the temporal hemifields were masked off, though responses were sometimes a little better. We conclude that the vergence responses to radial flow result from a true parsing of the flow pattern and not from anisotropies in motion detection.

Two other types of eye movement can be elicited with similar ultra-short latencies by large-field visual stimuli. There are indications that they too help to compensate specifically for translational disturbances of the observer1. The first employs conjugate eye movements (often termed ‘ocular following’) to track binocular motion in the plane of fixation as though compensating for lateral or vertical disturbances in the frontoparallel plane13–15, and the second employs vergence eye movements to eliminate binocular misalignments using binocular disparity cues (‘disparity vergence’) and so, like the radial-flow vergence described here, deals with

**Figure 1** Initial vergence responses to looming steps (radial optic flow plus size change). 

(a) Centrifugal pattern of optic flow experienced by an observer moving forwards (towards the black dot at the foot of the mountain). The amount of convergence required to maintain binocular alignment during forward movement is inversely related to the viewing distance, so the vergence required with the distant viewing depicted here would be minimal. Our experiments were all conducted with near viewing. 

(b) Mean horizontal and vertical vergence velocity profiles of subject GSM in response to looming steps simulating sudden decreases in the viewing distance of 1–8% at time zero. Upwards deflections indicate increased convergence and left sursumvergence. Calibration bar, 2

**Figure 2** The adequate stimulus for the short-latency vergence associated with looming steps is radial flow and the size changes are irrelevant. 

(a–c) Stimuli used (not drawn to scale) to test the dependence of vergence on radial flow and size change. 

(a) Radial flow plus size change (each dot shifts peripherally and enlarges). 

(b) Radial flow alone (each dot shifts peripherally but stays the same size). 

(c) Size change alone (each dot enlarges in place). 

(d) Mean vergence-velocity profiles of subject FAM in response to the three types of stimuli applied at time zero (simulating 4% reduction in the viewing distance). Upwards deflections indicate increased convergence. Calibration bar, 2° s⁻¹. All profiles are means of at least 138 responses.
front-to-back disturbances\textsuperscript{11,16}. Radial-flow vergence shares an additional property with these other ocular responses—transient post-saccadic enhancement—whereby stimuli applied (as here) in the immediate wake of a saccadic eye movement are much more effective than the same stimuli applied several hundred milliseconds later\textsuperscript{11,13}. In all cases, the post-saccadic enhancement is at least partly visual in origin, resulting from the reaffecter visual stimulation created by the saccade as it sweeps the image of the pattern across the retina: all show a similar (though often somewhat weaker) transient enhancement in the wake of a saccade-like shift of the large-field pattern. Appropriate large-field stimuli have also been shown to elicit ocular following\textsuperscript{17} and disparity-vergence\textsuperscript{16,18} responses in monkeys with properties often strikingly similar to those of humans.

Visual motion is processed mainly in the so-called dorsal stream of cortex\textsuperscript{5}. In monkeys, the medial superior temporal (MST) region of the cortex is the earliest stage at which global optic flow is encoded at the level of single neurons\textsuperscript{20–25}. Of particular interest here are MST neurons that are selectively sensitive to radial optic flow and do not respond to component size change\textsuperscript{26}. We suggest that all three types of eye movements elicited at ultra-short latencies are mediated by MST or its human homologue\textsuperscript{26}. In the case of ocular following, support comes from single-unit recordings and chemical lesions in monkeys\textsuperscript{7,16}. Putative ocular following neurons in MST respond to large-field motion in the frontoparallel plane with strong directional selectivity, being excited by motion in one direction and inhibited by motion in the opposite or orthogonal directions, thereby avoiding activation by radial flow\textsuperscript{5}. Such orthogonal inhibition might explain how the system could correctly attribute the flow experienced by our subjects to forwards, rather than to lateral, motion when exposure to the flow pattern was limited to one temporal hemifield. Recent recordings in MST have revealed neurons that discharge in relation to the short-latency disparity-vergence responses with disparity-tuning curves that exactly match the behaviour, unlike earlier stages in the cortical pathway to MST\textsuperscript{26}. In summary, we suggest that the flow-induced vergence described here is one of a family of visuallv driven eye movements in monkeys and humans that are elicited with ultra-short latencies, mediated by MST, and help to compensate specifically for translational disturbances of the observer.

**Figure 3** Effect of masking off various parts of the binocular visual fields on initial ocular responses of subject FAM to centrifugal optic flow. Insets indicate the extent of the masks: no mask (‘binoc. full field’), left eye masked (‘monoc. full field’), both nasal hemifields masked (‘binoc. hemifields’) and all but one temporal hemifield masked (‘monoc. hemifield’). In addition to the usual vergence velocity profiles (the difference between the velocity of the two eyes), the velocity profiles for each eye are shown, as well as the version velocity (the average velocity of the two eyes). All stimuli, simulating 4% reduction in viewing distance, occurred at time zero. Calibration bar, 2° s\textsuperscript{-1}. All profiles are means of at least 110 responses.

**Methods**

Most techniques have been described previously\textsuperscript{11,14}. The positions of both eyes were recorded using the electromagnetic search-coil technique\textsuperscript{16}. Subjects faced a vertical screen (viewing distance 33 cm; subtense, 80° × 80°) on which random-dot patterns (dot size, 1°) that filled the screen were back-projected from one of two slide projectors. The projected images were positioned with x/y mirror galvanometers and their presentation controlled by electromechanical shutters. Trials started with one pattern in place, and a target spot produced by a light-emitting diode (LED) was projected onto the screen, 10° to the right of centre. The subject was required to fixate this spot for a randomized time interval, after which the spot disappeared and a second appeared at the centre of the screen. Subjects were required to make a saccadic eye movement to this new spot, at which time it was switched off. With gaze now directed at the centre of the screen, after a post-saccadic delay of 50 ms the initial pattern was replaced with a new image (simulating the same pattern viewed from a different distance) produced by the second projector. After 200 ms the screen was blanked, ending the trial. Successive slides were carefully aligned so that the apparent focus of expansion (or contraction) was exactly at the centre of the screen and so imaged in the fovea. Applying optic flow stimuli after centring saccades took advantage of post-saccadic enhancement. For the hemifield experiments, four additional projectors were used with orthogonal polarizing filters in the projection paths to ensure that each eye saw only one hemifield\textsuperscript{16}. For monocular tests, one eye was occluded with a shutter that closed during the centering saccade.

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Defective limbic system in mice lacking the tailless gene

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The gene tailless is a member of the superfamilly of genes that encode transcription factors of the ligand-activated nuclear receptor type, and is expressed in the vertebrate and invertebrate brain1–4. In mice, its transcripts are restricted to the telencephalon, diencephalon, eye and nasal placode. To define the contribution of the tailless gene to mouse brain development and function, we have generated a targeted disruption of the gene by homologous recombination. The targeting strategy of the tailless locus is indicated (Fig. 1a).

We removed exons 2 and 3, which encode the two zinc-fingers (Fig. 1a). Homozygous animals were generated at the expected ratio by heterozygote crossing (Fig. 1b). Northern blot analysis revealed that the 3-kilobase (kb) tailless transcript was missing from mutant brains (results not shown), and RNase protection analysis confirmed that the sequences encoding the zinc-fingers were absent (Fig. 1c); some residual 3′ RNA did exist (exon 5; 20% of wild type; results not shown), however, probably as a result of inefficient termination signals in the neomycin-resistance gene or of alternative splicing around the insertion—either would cause a frameshift mutation. We concluded that the tailless gene had been effectively disrupted.

At birth, tailless mice are indistinguishable from their littersmates, but over their first three weeks they fail to gain weight normally, unlike mutant animals that are reared alone or hand-fed (Fig. 2a). Examination of ten brains from eight-week-old animals showed that all had a visible reduction in the size of their posterior cerebral hemispheres (Fig. 2c). Histological analysis revealed that the cytoarchitecture of the neocortex above the rhinal sulcus appeared to be normal; however, the so-called thalencephalon, including the piriform cortex, the islands of Calleja, the corticomedial amygdala, and the entorhinal cortex were markedly reduced (Figs 3, 4). Sections through the hippocampus revealed a much smaller dentate gyrus (Figs 3f, 4d, 5f) associated with a reduction and an abnormal lamination of the mossy fibre projection (Fig. 4f). The remainder of the hippocampus, the subfields CA3 and CA1, and the subiculum appeared normal. Pre- and parasubiculum were reduced or missing (Fig. 4f). The fornix and hippocampal commissure were abnormally shaped (not shown). The anterior commissure was also reduced, in particular its anterior wings connecting the olfactory cortices (Fig. 3d). Additional anatomical defects outside the limbic system were not found in the mice examined.