

inhibit neurogenesis in the adult human brain, we might eventually find a way to induce it in specific neurodegenerative disorders or following stroke and trauma, by blocking or bypassing the inhibition of mitotic activity. An additional benefit from discovering such inhibitory factors may be in the treatment of malignancy, where the goal is just the opposite, to prevent cell division. Finally, a promising approach may be the transplantation of stem cells to the affected brain areas. Recent grafting of human fetal neural stem cells into newborn mice demonstrates that such cells can both survive and, remarkably, migrate and differentiate into locally appropriate phenotypes—oligodendrocytes, astrocytes and neurons<sup>13,14</sup>. In these experiments, however, the host animals were newborns, in which the essential developmental cues are still preserved. For example, radial glial cell

scaffolding, an essential substrate for long-distance migration of the cortical neurons<sup>15</sup>, is absent in the adult cerebrum. It is therefore unclear whether transplanted neurons would migrate or differentiate appropriately in the adult brain. Furthermore, even if they do, this may not be sufficient to restore their function. Neurons in affected structures operate mainly through their precise, long-distance connections, which would also need to be re-established. To generate such connections in the large adult human brain may not be a trivial task. Nevertheless, the word impossible is not in the vocabulary of contemporary neuroscience.

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## Perception of heading is a brain in the neck

William H. Warren

How can you see where you are heading, given that your eyes and head can move relative to your body? Extra-retinal information about neck movements is part of the answer.

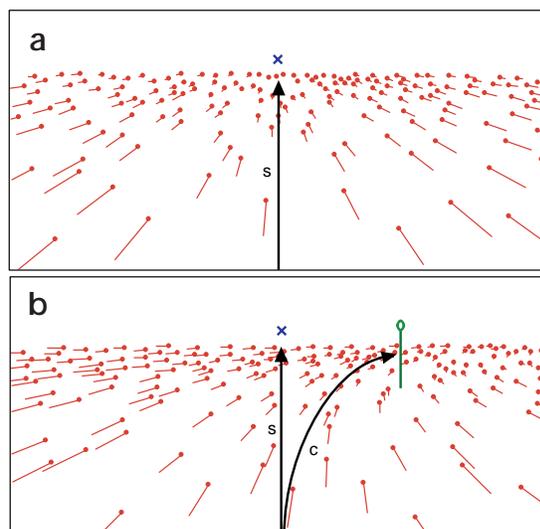
How do you see where you're going? As you move about the world, a pattern of motion called optic flow is generated at your moving eye. Somehow, from this flux of light, you are able to perceive your current path of travel, avoid obstacles, and reach your destination. The question of how this is done is of interest to psychologists studying perceptual-motor function, neuroscientists pursuing the underlying neural mechanisms, computer scientists building visually guided robots, and indeed anyone who can walk or drive.

One answer was proposed 50 years ago by James Gibson<sup>1</sup>. He noted that when you travel on a straight path, the optic flow necessarily forms a radial pattern with a focus of expansion lying in your current direction of self-motion or head-

ing (Fig. 1a). Consequently, you could use this focus as a 'point of aim' to steer toward goals and around obstacles. In practice, however, things are more complicated, because this flow pattern must

be detected by a mobile eye in a mobile head. To use optic flow as a source of directional information, the system must somehow compensate for these movements. Previous work has shown that extra-retinal information about movements of the eye within the head contributes to the perception of heading. In this issue (pages 732–737), Crowell, Banks, Shenoy and Andersen report the striking finding that the visual system also makes use of extra-retinal information about head turns.

To visualize the problem, imagine trying to build a robot that can guide itself through the world based only on visual information from a video camera. When the robot travels on a straight path, the

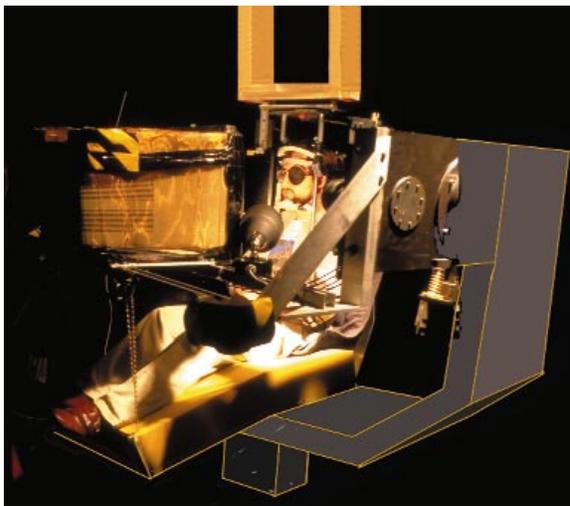


**Fig. 1.** Examples of retinal flow fields for travel parallel to a ground plane. Each vector represents the instantaneous retinal velocity of a point in the environment. **(a)** Radial velocity field produced by translation on straight path (s). The focus of expansion lies at the 'X'. **(b)** Velocity field produced by simultaneous translation on straight path (s) and rotation about a vertical axis to fixate the 'O'. The same instantaneous flow field is produced by travel on circular path (c), while looking along the tangent to the path.

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## news and views

**Fig. 2.** The experimental set-up used in the experiments by Crowell and colleagues. Subjects viewed an optic flow display while in a motorized dentist's chair. This allowed the authors to manipulate active and passive head and body rotations, and thus isolate the contributions of different sources of extra-retinal information. Photograph provided by James Crowell.



motion on the video screen forms a radial pattern like that of Fig. 1a—the ‘translational component’ of flow. This pattern will be familiar to anyone who has seen *Star Wars* and watched the Millennium Falcon catapult into hyperspace. In the last ten years, research in visual perception has shown that humans judge their direction of heading from such radial flow patterns with an accuracy better than 1 degree of visual angle<sup>2,3</sup>. At the same time, neuroscientists located an area in the visual cortex of the macaque monkey, known as MSTd, that contains neurons selective for specific kinds of flow patterns, including expansion, rotation and spiral motion<sup>4,5</sup>. Ken Britten and colleagues recently reported that microstimulation of MSTd biases the macaque’s heading judgments<sup>6</sup>, suggesting that this area may indeed mediate the perception of heading.

Now imagine that the robot is simultaneously rotating its camera to track an object in the scene, for example fixating on a stop sign while moving down the street. This dramatically alters the flow pattern on the screen (Fig. 1b) because the ‘rotational component’ destroys any special feature of the flow field in the direction of translation. How can the robot see which way it is heading in this case? In principle, such flow patterns could be analytically decomposed into their translational and rotational components. Numerous computational models have been derived for solutions based on retinal flow, many of them predicated on the fact that motion parallax is unaffected by rotation<sup>7,8</sup>. If, however, the robot had access to non-visual information about how fast its motors were turning the cam-

era, this could be used to estimate the rotational component independently. In such an extra-retinal solution, the rotation could then be subtracted from the flow pattern to recover the translation.

There is evidence, much of it from Banks’ lab<sup>9,10</sup>, showing that the visual system does indeed use extra-retinal information about eye movements to recover heading. When people are shown computer displays that simulate a combined forward translation and rotation over a random-dot ground plane and asked to judge their future path of travel, they tend to make large heading errors that increase with the simulated rotation rate (at >1 degree/s). As one might suspect from looking at Fig. 1b, observers typically report traveling on a curved rather than a straight path<sup>11</sup>, suggesting that they cannot recover the direction of translation from the flow pattern alone. However, when they make an actual pursuit eye movement to track a point in a radial flow display, heading errors are small, indicating that the visual system makes use of extra-retinal information about eye movements. It is known that MSTd neurons receive eye movement signals, and recent work in Andersen’s lab<sup>12</sup> has shown that in a subset of MSTd expansion-sensitive neurons, the preferred focus of expansion actually shifts within the receptive field during a pursuit eye movement, in a manner that would partially compensate for the rotation.

What is startling about the report of Crowell and colleagues is that extra-retinal information about something as remote as the neck can have the same role. The authors use a similar perceptual protocol, in which their subjects view a ran-

dom-dot display simulating translation and rotation. This time, however, they compare this condition with an actual head turn to track a point in a radial flow display. As with eye movements, they find that an active head rotation yields very accurate judgments of the future path.

In this case, there are three possible sources of extra-retinal information—proprioceptive information from the neck muscles, efferent information about the motor commands to the neck muscles, and vestibular canal information about head rotation. By cleverly manipulating active and passive head and body rotations, the authors are able to titrate out most of these sources. For example, vestibular information was isolated by having subjects view a radial flow display while the full body was passively turned in a motorized dentist’s chair (with no neck movement; see Fig. 2). Similarly, neck proprioception was isolated by fixing the head in a headrest and rotating the chair underneath it (together with the radial flow display), while keeping the neck muscles relaxed. To add efferent information to this situation, the head was freed and the subject was required to make active head turns to keep a head-mounted laser pointer on a stationary target, while the motorized chair (and display) counter-rotated underneath.

Contrary to what might have been expected, efferent information was not required to compensate for the rotation in half the subjects. Neither neck proprioception nor vestibular information alone was sufficient, and the combination of two sources yielded mixed results, typical of such ‘cue conflict’ situations; yet all three together produced accurate judgments in nearly all observers. One would like to understand the nature of these interactions and the origin of individual differences in more detail. The authors provide an important clue by showing that the combined effect of this information was not simply additive, ruling out a traditional linear model of ‘cue combination’.

Taken together, such extra-retinal research points toward a consistent picture in which movements of the eye in the head and the head on the body are simply compensated by extra-retinal information—as if we only gave our robot non-visual information about the camera turns. However, I think such a picture would underestimate the role of visual information in solving the problem. This claim hinges on the

demonstration that it is possible, at least under some conditions, for observers to separate translation from rotation on the basis of retinal flow information alone<sup>13</sup>. We have recently shown that simulated rotation displays of realistically textured scenes (which contain denser motion parallax than random-dot displays) yield quite accurate heading judgments in most observers<sup>14</sup>. These results are consistent with a model that relies on local motion parallax information<sup>7</sup>.

This finding is more remarkable when one considers that all simulated rotation displays are actually ambiguous; the velocity field in Fig. 1b may correspond to a straight path (s), or a circular path (c), or indeed any of a family of curved paths together with an eye or head rotation. Our observers thus report straight paths with small errors even when the display is ambiguous and the extra-retinal information specifies no eye or head rotation (consistent with a circular path). This suggests that the visual system tends to extract the translational component when sufficient motion parallax is available. Further, when the ambiguity is resolved by telling observers outright that

they are traveling on a straight path, heading judgments are consistently accurate, and conversely when they are told they are traveling on a curved path, errors become predictably large<sup>15</sup>. I believe this convincingly demonstrates that the visual system has the capacity to decompose translation from rotation on the basis of retinal flow information alone.

Crowell and colleagues have shown that extra-retinal information about head turns as well as eye movements contributes to the perception of heading with a mobile eye in a mobile head. A natural question is whether such information about the neck also acts to modulate MSTd receptive fields in monkeys. Researchers might similarly investigate MSTd responses to more realistically textured displays of simulated translation and rotation, in addition to random-dot displays. I suspect that the visual system makes use of both retinal flow and extra-retinal solutions<sup>3</sup>, as they are normally both available in everyday locomotion, but precisely how these processes are entwined in the recovery of heading remains to be disentangled.

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## Light detection: who needs eyes?

The blind mole rat (*Spalax ehrenbergi*) is a short-legged, mole-like rodent that lives entirely underground. Presumably as a result of this subterranean lifestyle, its eyes are atrophied and covered over by skin. The retina contains very few ganglion cells, and brain structures involved in image processing are either absent or dysfunctional. However, it does have functional suprachiasmatic nuclei, the site of the primary biological clock in mammals. On page 655, Russell Foster and colleagues (University College London) show that these 'blind' mammals actually sense light and regulate their body clocks accordingly.

The authors isolated a functional cone-like pigment from the degenerate eye of the blind mole rat, which they show entrains circadian rhythms to light. In the laboratory, upon entrainment to a 12:12 light/dark cycle, the majority of animals show greater periods of spontaneous locomotor activity (running on a wheel) during the subjective day. When the animals are then given a 15-minute light flash, they entrain their activity to this single stimulus. Most animals then become active before the pulse, almost as though they were anticipating 'dawn'. When the eyes are removed, this photoentrainment does not occur.

In the wild, blind mole rats are solitary and highly territorial. They dig extensive burrows with separate nesting, storage and defecation sites. During the breeding season, females build 'breeding' mounds, surrounded by smaller mounds connected via tunnels that the males occupy. Their habits raise a question: how would they be exposed to light outside the laboratory? The best guess is that this happens during mound building when they clear debris from their tunnels.

Photo courtesy of Tania Joyce

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