

84 Optic Flow

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OPTIC FLOW IS THE PATTERN of motion present at the eye of a moving observer. Such flow patterns contain information about self-motion, moving objects, and the three-dimensional (3D) layout of the environment, and could potentially be exploited to control locomotion. The term was first used by Gibson (1950) to generalize Helmholtz's notion of *motion parallax* from single objects to the continuous environment surrounding the observer. He developed the concept during World War II while working on methods for pilot testing and training, after he concluded that the classical depth cues were inadequate to explain a pilot's practical ability to land an airplane. But little research was done on the subject until the 1980s, when its relevance to robot and vehicle guidance was recognized and computer animation made it amenable to study.

Optic flow is a key example of Gibson's (1979) *ecological approach* to perception and action. This functionalist approach emphasizes that the task of vision is to guide successful behavior in the natural environment, and stresses the importance of higher-order optical information that specifies complex properties of that environment and its relationship to the observer. The nervous system is viewed as providing causal support for the detection of informational variables and the modulation of action variables. Optic flow offers a case study of a higher-order variable that has been formally analyzed and empirically investigated in some detail. In what follows, we will trace optic flow through the cycle of perception and action.

The past 20 years have seen intensive research on the topic, with parallel developments in the domains of human perception, primate neurophysiology, and computational vision. This chapter aims to integrate these perspectives to address both mechanistic questions about how optic flow patterns are extracted by the visual cortex and functional questions about how this information is used to perceive self-motion and control behavior. (For related reviews see Lappe et al., 1999; Warren, 1998; regarding structure from motion, see Todd, 1995.)

The optic flow field

Optic flow is typically represented as an instantaneous velocity field in which each vector corresponds to the optical motion of a point in the environment, as in Figure 84.1A. It is immediately apparent that this flow field has a radial struc-

ture, with a *focus of expansion* (FOE) lying in the direction of self-motion. When one views the moving display, it is also apparent that the environment is a planar surface receding in depth. The radial pattern of vector directions depends solely on the observer's direction of translation, or *heading*, and is independent of the 3D structure. The magnitude of each vector, on the other hand, depends on both heading and depth and decreases quickly with distance. The radial flow pattern thus specifies one's current heading, whether or not the local FOE itself is visible. This was Gibson's fundamental hypothesis about the perception of self-motion from optic flow, and was the starting point for both psychophysical and neurophysiological experiments.

Although the velocity field description is compatible with the motion selectivity of cortical areas V1 and MT, it does not represent higher-order temporal components of the optic flow such as acceleration, or the trajectories of points over time. This appears to be a reasonable approximation, for the visual system is relatively insensitive to acceleration and relies primarily on the first-order flow to determine heading (Paolini et al., 2000; Warren et al., 1991a).

OBSERVER ROTATION However, the detection of optic flow by a moving eye is complicated by the fact that the eye can also rotate (Gibson, 1950, pp. 124–127). If the observer simply translates on a straight path, the flow pattern on the retina is radial (Fig. 84.1A). This is called the *translational component* of retinal flow, and recovery of heading from it is straightforward. A rotation of the observer, such as a pursuit eye or head movement, merely displaces the image on the retina, producing the *rotational component* of retinal flow.¹ Specifically, pitch or yaw of the eye create patterns of vertical or horizontal lamellar flow (Fig. 84.1B), and roll about the line of sight creates a pattern of rotary flow. But if the eye is simultaneously translating and rotating, which commonly occurs when one fixates a point in the world during locomotion, the retinal flow is the vector sum of these two components (Fig. 84.1C). The resulting flow field is more complex, without a qualitative feature corresponding to

¹To keep these distinctions clear, I will consistently use *translation* and *rotation* to describe observer movement and *lamellar* and *rotary* to describe flow patterns.

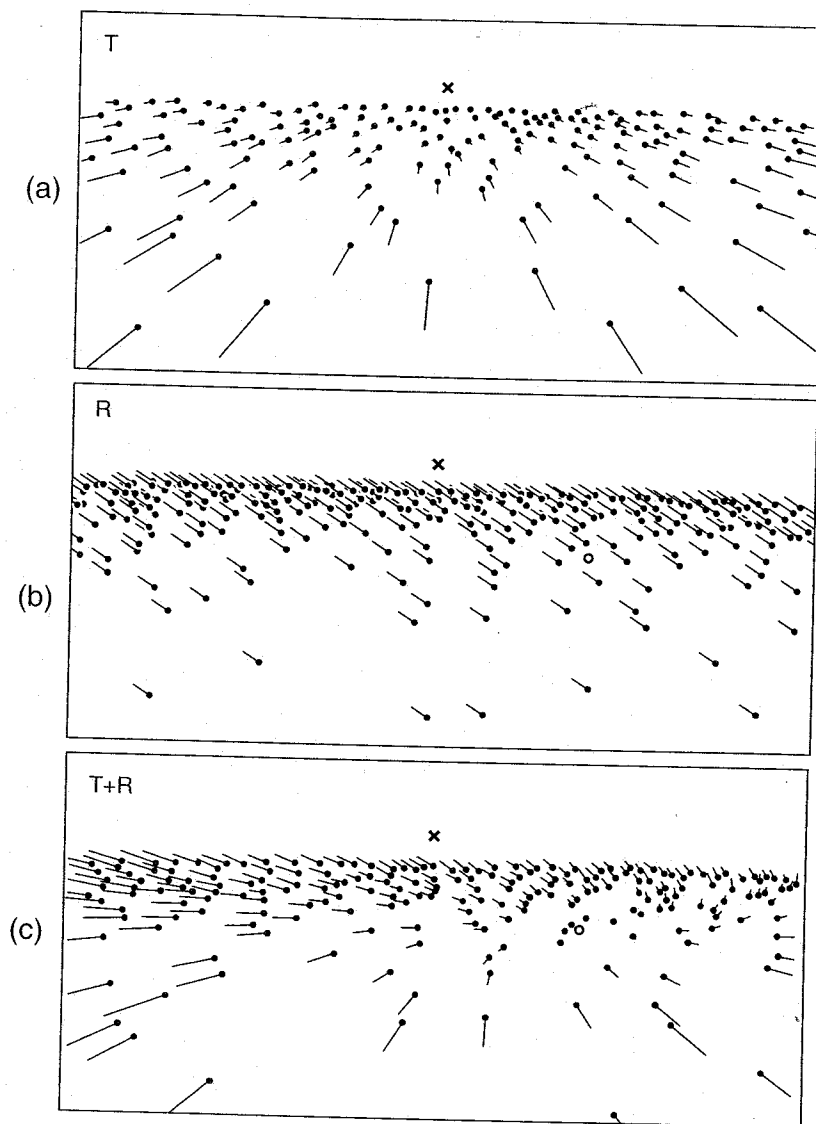


FIGURE 84.1. Retinal flow field for a ground plane with rotation about a diagonal axis. *a*, Translational component produced by observer translation toward the x : radial flow from the heading point. *b*, Rotational component produced by eye rotation downward and to the right: lamellar flow upward and to the left. *c*, Flow field

produced by the sum of *a* and *b* due to heading toward the x while rotating to track the O on the ground plane. The singularity in the field is now at the fixation point. Note the motion parallax (differences in vector direction and length) at different distances across the surface.

one's heading; indeed, the singularity in the flow field is now at the fixation point.

Thus, to determine heading, the visual system must somehow analyze the translational and rotational components and recover the direction of self-motion. This has come to be known as the *rotation problem*. Fortunately, the retinal flow in a 3D scene contains sufficient information to solve this problem in principle. Specifically, *motion parallax between points at different depths corresponds to observer translation*, whereas *common lamellar motion across the visual field corresponds to observer rotation*.

THE PATH OF SELF-MOTION Even if the rotation problem can be solved, however, it only yields one's instantaneous

heading. A further problem is that the velocity field does not specify one's path over time—for instance, whether one is traveling on a straight or a curved path. In fact, the same flow field can be generated by a straight path together with eye rotation or by a circular path of self-motion. A particularly troublesome case appears in Figure 84.2, in which translation plus rotation about a vertical axis produces the same velocity field as a circular path on the ground plane. When presented with such flow displays, observers often report seeing a curved path of self-motion rather than a straight path plus rotation. How, then, can one determine whether one is traveling on a straight or a curved path? We will call this the *path problem*.

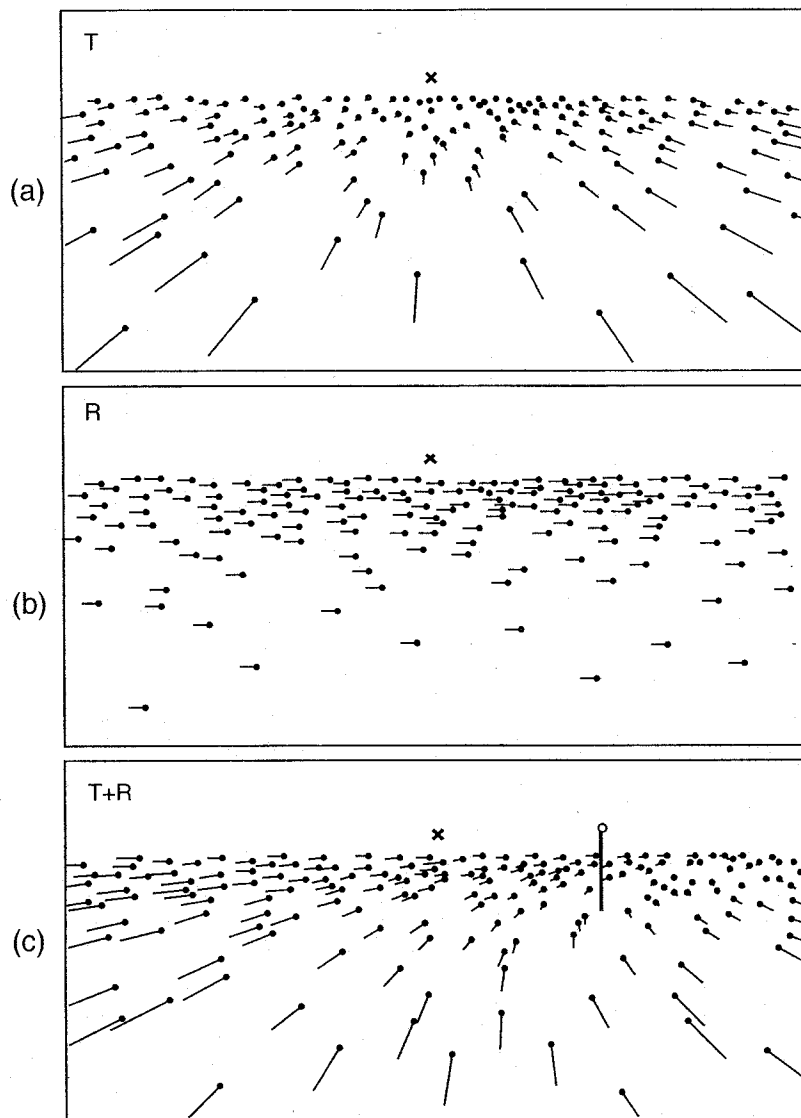


FIGURE 84.2. Retinal flow field for a ground plane with rotation about a vertical axis. *a*, *Translational component* produced by observer translation toward the *x*. *b*, *Rotational component* produced by eye rotation to the right. *c*, Flow field produced by the sum of *a* and *b* due to translating toward the *x* while rotating to track the *O* on the post, which is at eye level. An identical velocity field is generated by travel on a circular path to the right, with instantaneous heading along the tangent toward the *x*.

Before tackling these issues, let's consider the detection of optic flow patterns.

Detecting optic flow

From a mechanistic point of view, the basic question is how optic flow is detected by the visual system. It now appears that optic flow patterns are extracted in two steps, by first detecting local motion and then integrating it spatially in units sensitive to patterns of motion. This can be demonstrated psychophysically using random-dot displays in which the proportion of "signal" dots moving in a coherent flow pattern is varied relative to "noise" dots that jump to random positions on each frame. As the area of coherent motion in

the display increases, the direction of motion can be reported at a lower signal-to-noise ratio, providing evidence of spatial summation (Burr et al., 1998). Such coherence thresholds reveal summation for radial, rotary, and lamellar flow patterns over large visual angles up to 36 to 72 degrees. The data are closely predicted by an ideal integrator that pools local motion signals in units sensitive to pattern motion with large receptive fields.

FLOW-SELECTIVE UNITS IN MSTd Such findings converge with results from single-cell recordings in the dorsal region of the medial superior temporal area (MSTd) of macaque visual cortex (see Chapters 83 and 85, this volume). Saito et al. (1986) reported cells selective for expansion or con-

traction, clockwise or counterclockwise rotary flow, or directional lamellar flow, and proposed that they could be constructed by integrating input from velocity-selective cells in area MT. The MSTd cells are characterized by large receptive fields 15 to 65 degrees in diameter, distributed over the visual field to eccentricities of 50 degrees, with a higher concentration closer to the fovea (Raiguel et al., 1997). These cells exhibit stronger responses to larger stimulus patterns, consistent with spatial integration of local velocity signals (Duffy and Wurtz, 1991b; Tanaka and Saito, 1989).

About half of MSTd cells are selective for radial or rotary flow at various locations in their receptive fields, a property known as *position invariance*. Rigorous tests of position invariance ensure that a cell's response is not simply due to a coincidental match between the stimulus and a local region of the receptive field (Lagae et al., 1994). This finding is consistent with an architecture in which clusters of velocity-selective MT cells, each having a radial or rotary arrangement at different retinal loci, converge on one MSTd cell.

Such radial and rotary cells are also broadly tuned to the overall speed of motion, so that they may form a distributed representation of mean flow speed (Orban et al., 1995; Tanaka and Saito, 1989). There are also indications of sensitivity to speed gradients within the flow pattern, with some cells preferring an increasing gradient from center to periphery and others preferring a decreasing gradient (Duffy and Wurtz, 1997). However, the gradients tested were quite extreme, and MSTd cells are relatively insensitive to the fine speed gradients needed to distinguish 3D shape. Eliminating the pattern of vector directions has a far greater impact on a cell's response than eliminating the speed gradient (Tanaka et al., 1989).

MST projects to higher areas in the dorsal visual pathway, including parietal area 7a. Cells in this area are more narrowly tuned to radial, rotary, spiral, and lamellar flow patterns (Siegel and Read, 1997), indicating that the processing of optic flow continues beyond MSTd.

DECOMPOSITION OR TEMPLATES? There has been a great deal of interest in the hypothesis that specialized channels in MSTd form a basis set for the decomposition of optic flow. Koenderink and van Doorn (1975, 1981; Longuet-Higgins and Prazdny, 1980) showed that any optic flow field can be analyzed locally into lamellar motion plus three elementary components: *divergence* (div) or rate of local expansion, which together with surface slant can be used to estimate heading; *curl* or rate of local rotary flow; and *deformation* (def) or rate of shear along two orthogonal axes, which is specific to surface shape. This insight inspired a number of studies on sensitivity to radial, rotary, and lamellar flow in MSTd. However, there is often confusion between divergence and radial flow. Formally, div is a measure of the local rate of expansion, not the radial motion pattern or the FOE.

The balance of psychophysical research does not support decomposition into div, curl, def, and lamellar motion. For example, when the div is removed from an expansion pattern, resulting in radial flow with decelerating dot motion outward from the FOE, the detection thresholds for expansion in noise are unaffected (Kappers et al., 1996). Such results are contrary to a specialized divergence detector. Although the maximum of divergence can be located in visual displays (Regan and Beverly, 1982), there is no evidence that it is actually used to judge heading (Warren et al., 1988).

Similar conclusions have emerged from single-cell recordings in MSTd. When cells selective for radial or rotary flow are presented with a spiral flow pattern containing both div and curl components, the response is lower than with the equivalent radial or rotary pattern alone (Orban et al., 1992), indicating that the spiral flow is not decomposed. A majority of cells are not tuned to a single elementary component but respond to two or three individual components (Duffy and Wurtz, 1991a) or to combinations of radial and rotary flow (Graziano et al., 1994). There thus appears to be a continuum of cells selective not only for radial and rotary flow but also for intermediate spiral flow patterns.

Taken together, the evidence indicates that MSTd cells do not decompose optic flow into elementary components, but rather act as templates or filters for complex flow patterns. The advantage of a template mechanism is that, rather than simply recoding the information in the flow field, its response can signal the presence of meaningful patterns of stimulation.

Perception of translational heading

From a functional point of view, the primary question about optic flow is whether people can in fact perceive their self-motion from optic flow patterns. Cutting et al. (1992) estimated that a heading accuracy of about 1 to 3 degrees is required to guide ordinary locomotion such as running and skiing. When observers view a random-dot display of radial flow and judge whether they are heading to the left or right of a probe, they are highly accurate, with heading thresholds as low as 0.5 degree (Warren, 1976; Warren et al., 1988). Translational heading can thus be perceived from radial flow with sufficient accuracy to control locomotion.

SPATIAL INTEGRATION Heading judgments also reveal spatial integration, similar to simple coherence thresholds. In principle, a heading estimate could be obtained by triangulating just two motion vectors in a radial flow pattern. However, such a mechanism would be vulnerable to noise in local motion sensors, leading to large heading errors (Koenderink and van Doorn, 1987). Since each vector provides an estimate of the heading, pooling them allows this

redundancy in the flow pattern to reduce triangulation error. Consistent with such pooling, heading thresholds decrease as dots are added to a radial flow display, following a $1/\sqrt{N}$ rule, up to an asymptote with about 30 dots in a 40×32 degree display (Warren et al., 1988). Heading judgments are also highly robust to flow field noise created by perturbing vector directions (Warren et al., 1991a). Both of these properties are reproduced by a simple neural model of translational heading in which local motion signals are pooled in large-field radial flow templates (Hatsopoulos and Warren, 1991), consistent with the spatial integration observed in MSTd.

FLOW STRUCTURE AND SPEED GRADIENTS In line with the fact that the radial structure of flow is independent of depth, heading thresholds are similar in different 3D environments, including a ground plane, a frontal plane, and a cloud of dots. Judgments even remain accurate when speed gradients are removed by randomizing the magnitudes of local vectors, preserving their directions, but they become impossible when vector directions are randomized, preserving their magnitudes (Warren et al., 1991a). This result confirms the primary importance of the pattern of vector directions and is strikingly consistent with MSTd responses (Tanaka et al., 1989). However, heading judgments are influenced by large speed gradients. If vector magnitudes on one side of the FOE are greatly increased, perceived heading is biased toward the opposite side, and subjects report travel on a curved path (Dyre and Andersen, 1996). This is plausible because, in a homogeneous environment, the pattern of flow speeds is correlated with the path of travel. On a straight path, vectors tend to increase symmetrically from the FOE (Fig. 84.24), whereas on a curved path, vectors on the outside of the path tend to be greater than those on the inside (Fig. 84.2C).

HEADING IN THE PRESENCE OF MOVING OBJECTS Most optic flow analyses presume a rigid scene, yet we locomote successfully in a dynamic environment with independently moving objects. A moving object can significantly alter the radial flow pattern, creating a local region of inconsistent motion. To cope with this, the visual system might segment the scene and make separate estimates of self-motion from the background flow and of object motion from the discrepant flow (Hildreth, 1992). A simpler solution would be to estimate the FOE by pooling all motion vectors, consistent with spatial integration in MSTd, although this would lead to predictable heading errors.

In fact, heading judgments exhibit just such errors when the object crosses the FOE (Warren and Saunders, 1995). If the object is moving in depth, it creates a piece of a radial flow pattern with a secondary FOE. This is enough to bias perceived heading *opposite* the direction of object motion by

a few degrees toward the FOE. Such an effect is consistent with spatial integration of all motion to locate the FOE. However, if the object is moving in the frontal plane, it creates a piece of lamellar flow, which biases perceived heading in the *same direction* as object motion (Royden and Hildreth, 1996). This effect is similar to an illusory shift in the FOE that occurs when a lamellar flow pattern is transparently superimposed on a radial flow pattern (Duffy and Wurtz, 1993) and could be a consequence of using lamellar flow to estimate observer rotation (Lappe and Duffy, 1999). On the other hand, both effects might also be explained as a result of pooling the motion parallax between the object and the background together with the local dot motions, which could be a consequence of using motion parallax to recover heading.

These results lead to the surprising conclusion that moving objects are not segmented in the course of perceiving heading, and suggest that self-motion relative to the environment may be determined by a task-specific mechanism that responds to any flow within its receptive field. MSTd cells might provide such a mechanism, for they respond selectively to a given flow pattern whether it is carried by a large field of random dots or the local boundary of a square (Geesaman and Andersen, 1996). This suggests that MSTd detects flow patterns produced by relative motion between the observer and the environment, without differentiating local object motion.

IS SELF-MOTION DETERMINED IN MSTd? Selectivity for large-field radial, rotary, and lamellar flow patterns and their combinations makes MSTd a likely candidate for extracting information about self-motion. Such global motion patterns are generated by observer translation, roll, and pitch/yaw with respect to the environment. As we have seen, there are a number of commonalities between the characteristics of MSTd cells and heading judgments: (1) large receptive fields suitable for global flow, (2) spatial integration, (3) dominance of vector directions but also (4) responses to large speed gradients, (5) speed tuning that could code the velocity of observer translation or rotation, and (6) failure to differentiate local object motion and global flow.

At first blush, the position invariance of MSTd cells appears inconsistent with this hypothesis, for heading detection by single cells implies a preferred locus for the FOE in the receptive field. However, this objection confuses response selectivity with response amplitude. Duffy and Wurtz (1995) found that 90% of expansion cells do have a preferred FOE and exhibit a graded response as the focus is shifted away from this position, which is well fit by a Gaussian tuning curve (Raiguel et al., 1997). A population of such cells is in principle sufficient for a precise distributed coding of heading direction. A second issue is that MSTd cells do not appear to form a contiguous retinotopic map of heading

direction. Nevertheless, similarly tuned cells tend to be clustered together in approximate cortical columns (Britten, 1998), which is not incompatible with distributed coding.

The most direct evidence that MSTd is involved in heading is that microstimulation in a cluster of cells biases radial flow localization judgments in the direction preferred by nearby cells in two-thirds of cases (Britten and von Wezel, 1998). The conclusion is reinforced by the finding that vestibular stimulation produced by physically translating the animal modulates the response amplitude and even the direction preference to radial flow in MSTd cells (Duffy, 1998). This strongly implies that MSTd is a site that integrates sensory stimulation about self-motion.

In humans, brain imaging studies indicate that a possible homolog of MSTd, an inferior satellite of MT/V5, is selective for radial and rotary flow patterns (Morrone et al., 2000). Using an active judgment task, Peuskens et al. (2001) found that attending to heading per se enhanced specific activity in this MT/V5 satellite, as well as in a posterior region of the dorsal intraparietal sulcus (a possible homolog of area 7a) and in dorsal premotor cortex. These results suggest that heading is detected in a pathway that is functionally similar to primate areas MSTd and 7a and directly related to motor behavior.

The rotation problem

Determining heading from radial flow during pure translation is relatively straightforward. But when the observer also makes a pursuit rotation of the eye or head, a component of lamellar flow is added, radically altering the retinal flow field (Fig. 84.2C). How, then, might the instantaneous direction of heading be determined during rotation? There are two general approaches to the rotation problem.

EXTRARETINAL THEORIES Extraretinal theories propose that internal signals about the rotational velocity of the eye and head, possibly including efferent, proprioceptive, and vestibular signals, are used to estimate the rotational component of self-motion (Banks et al., 1996; Royden et al., 1994). The rotational component can then be subtracted from the retinal flow pattern in order to recover the translational component and hence the instantaneous direction of heading. If any rotation remains in the flow pattern, it can be attributed to a curved path of self-motion. Note that the resulting heading estimate is in retinal coordinates, or an *oculocentric* frame of reference. Thus, extraretinal signals about the position of the eye and head may also be needed to transform the heading into *head-centric* and *body-centric* reference frames.

A possible mechanism for extraretinal theories is dynamic tuning of receptive fields in MSTd. During a pursuit eye movement, the preferred FOE tuning of most expansion

cells actually shifts on the retina in the direction of rotation, partially compensating for pursuit (Bradley et al., 1996). However, the mean shift is only half of what is needed to compensate fully for the eye movement. Some cells show no shift at all, but rather a modulation in the amplitude of their response, consistent with the notion of a *gain field* (Shenoy et al., 1999). On the other hand, Page and Duffy (1999) reported that a computed population vector fully compensates for pursuit rotation and might be "read out" by a higher area. Area 7a contains cells that are narrowly tuned to radial flow and show gain modulation by eye position (Read and Siegel, 1997), potentially converting an oculocentric heading estimate into a head-centric frame.

Physiological results would thus seem to support an extraretinal approach. However, Shenoy et al. (1999) found large receptive field shifts in response to the flow pattern alone, even when the eye was stationary. This suggests that partial compensation can occur on the basis of the retinal flow itself. Moreover, these experiments only tested planar (non-3D) flow patterns, and compensation might be greater with motion parallax in the display. This leads us to the second approach.

RETINAL FLOW THEORIES Gibson argued that the optical information available in natural environments is sufficient for visual perception, and was skeptical of the need for extraretinal signals. Retinal flow theories propose that heading can be determined from the pattern of retinal flow alone (Warren and Hannon, 1990). This is theoretically possible because observer rotation simply adds a common lamellar component to the flow field, such that the differential motion due to translation remains invariant. Numerous computational models have formally shown that instantaneous heading can be recovered from the velocity field during rotation (see Hildreth and Royden, 1998; Warren, 1998, for reviews). As before, this heading estimate is in an oculocentric frame of reference, so extraretinal position signals would seem to be necessary to convert it to head-centric and body-centric reference frames to recover one's *absolute heading* in space. But such coordinate transformations could be bypassed by determining one's *object-relative heading*, the direction of translation with respect to objects that are also registered in retinal coordinates. This is physiologically plausible because target position and optic flow analyses converge at least by area 7a.

There are three main classes of retinal flow theories. One class first estimates observer rotation from the lamellar flow, then subtracts the rotational component from the retinal flow pattern to recover the translational component (Perrone, 1992). In principle, the rotational component could be measured by integrating retinal velocities independently about three orthogonal axes (Koenderink, 1986). It is thus plausible that MSTd cells selective for horizontal,

vertical, and rotary flow patterns detect observer rotation; indeed, the preferred direction of pursuit eye movements in these cells is opposite the preferred direction of lamellar flow. Because the motion of more distant points is increasingly dominated by the rotational component (Fig. 84.2), depth information such as binocular disparity could also contribute to estimating the rotational component (van den Berg and Brenner, 1994).

A second class of theories determines the heading directly from motion parallax, which is also known as *relative* or *differential motion* (Longuet-Higgins and Prazdny, 1980; Rieger and Lawton, 1985). The relative motion between two points at different distances along a line of sight can be described by a difference vector. Remarkably, the set of difference vectors for a 3D scene forms a radial pattern centered on the heading. The rotation problem can thus be solved quite elegantly if there is sufficient depth structure in the environment. Moreover, relative motion and common motion could be extracted in parallel to decompose observer translation and rotation.

In theory, differential motion could be detected by an array of antagonistic center-surround units, with either circularly symmetric or bilateral center-surrounds (Royden, 1997). A majority of cells in area MT actually possesses such a bilateral opponent-motion organization, is sensitive to speed differences between center and surround, and is segregated in separate columns from classic MT velocity units (Born and Tootell, 1992; Xiao et al., 1997). Given that MT projects to MSTd, these two motion pathways could detect radial patterns of ordinary flow vectors and difference vectors in parallel, allowing the visual system to extract heading in both planar and 3D environments (Warren, 1998). Consistent with this idea, the responses of MSTd cells are enhanced by the addition of motion parallax in a radial flow display during fixation, and even more so during pursuit movements (Upadhyay et al., 2000). Thus, motion parallax signals contribute to activity in MSTd, especially during eye rotation, a finding that deserves further investigation.

A third class of theories is based on templates for the set of flow patterns produced by all possible combinations of observer translation and rotation (Lappe and Rauschecker, 1993; Perrone and Stone, 1994). The space of flow patterns is constrained by restricting rotations to pursuit of stationary points in the environment. Perrone and Stone (1998) showed that their model templates reproduce many properties of MSTd cells, including selectivity for radial, lamellar, and spiral flow, position invariance, and a preferred FOE.

PERCEIVING HEADING DURING ROTATION The psychophysical evidence on the rotation problem is mixed, and the issue remains controversial. In these experiments, displays are manipulated to dissociate retinal and extraretinal contributions. In the *actual rotation* condition, a radial flow pattern is

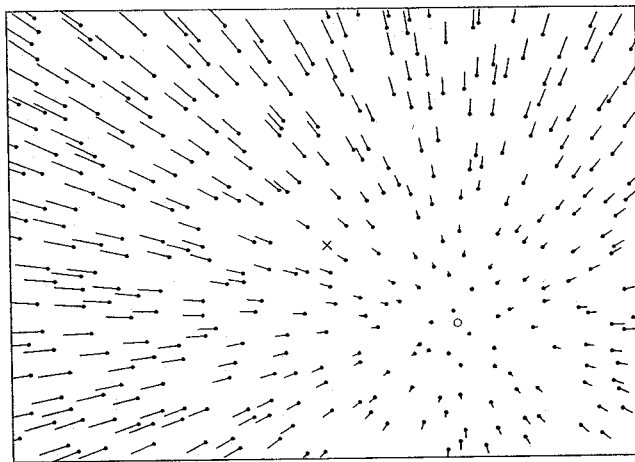


FIGURE 84.3. Retinal flow field for a frontal plane with rotation about a diagonal axis. The observer is translating toward the x while rotating to track the o on the plane downward and to the right. This produces a pseudo-FOE at the fixation point. Because the distance of the surface from the eye changes very little, only a little motion parallax is defined across a large display.

presented on the screen (Fig. 84.14) together with a moving fixation point that induces a pursuit eye movement; thus, extraretinal signals correspond to the rotation. In the *simulated rotation* condition, the flow pattern on the screen simulates the effect of forward translation plus a pursuit rotation (Fig. 84.1C) while the fixation point remains stationary, so extraretinal signals correspond to zero rotation. The flow pattern on the retina is thus the same in both conditions, while the extraretinal signal is manipulated. If judgments are equally accurate in the simulated and actual conditions, it implies that heading can be perceived from the retinal flow alone—even with conflicting extraretinal signals. On the other hand, if judgments are markedly less accurate in the simulated condition, it implies an extraretinal contribution.

Warren and Hannon (1988, 1990) reported that heading judgments with a random-dot ground plane (Fig. 84.1C) or 3D cloud were comparable in the two conditions, yielding heading thresholds below 1.5 degrees. On the other hand, with a frontal plane, which contains almost no motion parallax (Fig. 84.3), performance was at chance in the simulated condition but remained accurate in the actual condition. This pattern of results is consistent with retinal flow theories and confirms the importance of motion parallax. Observers even report an illusory eye rotation in the simulated condition corresponding to motion of the (stationary) fixation point away from the heading. But good performance with a frontal plane during actual eye rotation also indicates that extraretinal signals can contribute to heading judgments.

However, in these experiments the mean rotation rate over a trial was less than 1 deg/sec. At higher simulated rota-

tion rates (1 to 5 deg/sec),² heading judgments were subsequently found to be highly inaccurate (Banks et al., 1996; Royden et al., 1994). Constant errors rose to 15 degrees in the direction of simulated rotation but remained close to zero during actual eye rotation. This pattern of results is consistent with the extraretinal theory for high rotation rates. At the same time, other research supported a retinal flow theory (van den Berg, 1993; Wang and Cutting, 1999). Binocular disparity appeared to make heading judgments more reliable during simulated rotation (van den Berg and Breener, 1994), although Ehrlich et al. (1998) failed to replicate this effect.

Royden (1994) pointed out that observers frequently report a curved path of self-motion in the simulated rotation condition, and that heading errors in the direction of simulated rotation are consistent with the perception of a curved path. This might be expected from the ambiguity of the velocity field, for the same instantaneous field can be produced by a straight path plus rotation or by a circular path of self-motion with radius r (Fig. 84.2C), which are related by the ratio of translation and rotation speeds ($r = T/R$). Because extraretinal signals indicate that rotation is zero in the simulated condition, this could lead to the perception of a curved path. It is important to distinguish the concepts of *heading* and *path*, for although they are identical for a straight path, the instantaneous heading direction is tangent to a curved path. It is apparently difficult for observers to judge their instantaneous heading per se, for even when instructed to do so, they tend to report their perceived path. This leaves open the possibility that the oculocentric heading is accurately recovered during simulated rotation, but because the body-centric heading changes over time (literally drifting across the screen), subjects report a curved path.

One response to this dilemma was to try to elicit reports of instantaneous oculocentric heading by other means. When instructed to base heading judgments on the illusory motion of the fixation point, observers are more accurate than with path judgments of the same displays (van den Berg, 1996). This suggests that the visual system implicitly recovers heading during simulated rotation. When asked to judge the direction in which they are skidding while traveling on a circular path, observers' heading judgments also improve (Stone and Perrone, 1997), indicating that the instantaneous heading direction can be estimated.

Another response to the dilemma is to investigate the conditions for accurate path perception, since that is what observers tend to report.

The path problem

Observers can judge their prospective path of self-motion very accurately on a straight path, a circular path (Warren et al., 1991b), and even an elliptical path whose curvature changes with time (Kim and Turvey, 1998) from displays that simulate the view through the windshield of a turning car.³ A circular path can be parameterized by the instantaneous heading direction (\hat{T}), which is tangent to the path at the observation point, and the curvature of the path ($\kappa = 1/r$). Path curvature is equal to the rate of change in heading with respect to distance traveled ($\kappa = d\hat{T}/ds$), or with respect to time, scaled by translation speed ($\kappa = (d\hat{T}/dt)/T$). A higher-order path can be considered piecewise as a series of osculating circles, each of which is tangent to the path and defines a local path curvature.

We do not know how the visual system recovers curved paths of self-motion. The most straightforward solution is to determine the current body-centric heading and its rate of change, as just described. But contrary to this approach, path perception is quite accurate for windshield-like displays in which the body-centric heading doesn't change. This suggests a second solution: recovering the circular path directly from the flow field. A circular path on a ground plane generates a curved velocity field (Fig. 84.2C) that is stationary over time and uniquely corresponds to path curvature (for a constant eye height). The *locomotor flow line* that passes under the observer's feet specifies the oculocentric path (Lee and Lishman, 1977), and its location with respect to objects in the scene specifies the object-relative path. For higher-order paths, the flow field curvature changes over time with the path curvature. A third solution is to determine curvature from the ratio of rotation to translation speeds ($\kappa = R_p/T$), where R_p is the rotation attributed to path curvature after compensating for eye and head rotation (Ehrlich et al., 1998).

It is possible that spiral cells in MSTd code the path curvature from ground plane flow. It does not appear that extended paths are recovered by individual cells, for they respond similarly to a given flow pattern regardless of the one that precedes or follows it in a continuous sequence of stimulation (Paolini et al., 2000). Thus, single MSTd cells do not code for second-order temporal properties such as acceleration or changes in the flow pattern, but they could code the instantaneous path curvature.

RESOLVING THE PATH PROBLEM How, then, might one determine whether the path of self-motion is straight or curved from retinal flow alone? Li and Warren (2000) pro-

²A rotation rate of 1 deg/sec would be produced by fixating the ground plane 10 m ahead while walking at 1 m/sec and a 5 deg/sec rotation by fixating 4 m ahead.

³Specifically, the line of sight is along the tangent to the path, such that the instantaneous heading remains fixed on the screen.

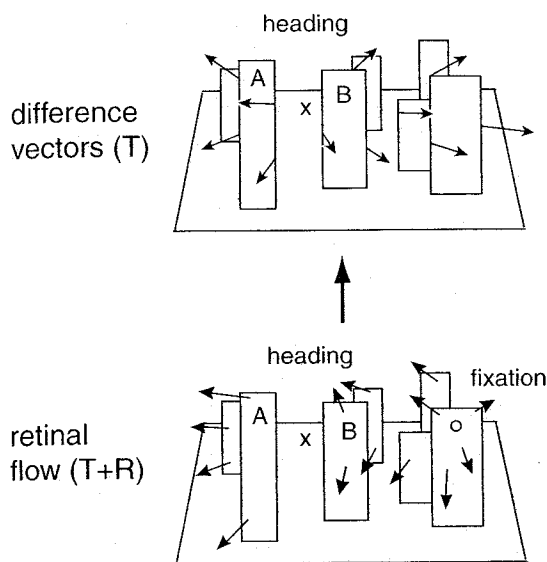


FIGURE 84.4. Object-relative heading. *Bottom*: Sketch of retinal flow in a complex scene. The observer is heading toward x while rotating rightward to track O . *Top*: Difference vectors from motion parallax specify the instantaneous heading. The current object-relative heading is a few degrees to the left of object B. If the path is straight, the heading will remain fixed in the scene over time; if the path is curved to the right, the heading point will shift rightward with respect to object B.

posed that the visual system updates the *object-relative heading* over time. Specifically, the visual system continually extracts the instantaneous heading with respect to objects in the scene, presumably on the basis of motion parallax (Fig. 84.4). The sequence of such headings over time traces out the observer's path through the environment. For example, if the path is straight, then the heading remains fixed in the scene, whereas if the path is curved, the heading shifts relative to objects over time.

This solution to the path problem requires sufficiently dense motion parallax for an accurate heading estimate and distinct reference objects in the scene that can be tracked over time. However, most previous research used random dots, which are necessarily sparse and not easily tracked. In contrast, when displays contain dense texture-mapped scenes with distinct objects, path judgments are reasonably accurate, with mean errors below 4 degrees at simulated rotation rates up to 7 deg/sec (Cutting et al., 1997; Li and Warren, 2000). This is also the case for active steering during simulated rotation (Li and Warren, 2002). Object-relative heading thus allows the visual system to determine the path of self-motion through the environment on the basis of retinal flow, even when it is in conflict with extraretinal signals.

The mixed results for heading judgments are probably a consequence of the cue conflict for path perception in the simulated rotation condition. Extraretinal signals

indicate that eye rotation is zero; hence, the rotational component of flow must be due to a curved path. But over time, the retinal flow specifies that object-relative heading is constant, so the observer must be traveling on a straight path through the depicted environment. If the visual system makes use of both retinal and extraretinal signals, it is not surprising that the data are inconsistent. But with distinct reference objects in the display, object-relative paths tend to dominate.

ROLE OF EXTRARETINAL SIGNALS The preceding evidence indicates that both retinal flow and extraretinal signals can contribute to heading and path perception. This raises the question of how retinal and extraretinal signals are related.

Recent results suggest that an extraretinal estimate of rotation is not simply subtracted from retinal flow; rather, the two interact nonlinearly (Crowell and Andersen, 2001; van den Berg et al., 2001). When real and simulated pursuit are in the same direction, extraretinal signals exert a partial influence, but when they are in opposite directions, there is little extraretinal influence. Moreover, if the retinal flow corresponds to a 3D scene (i.e., contains motion parallax or perspective), eye rotation is determined from the common lamellar flow, providing accurate pursuit compensation. Extraretinal signals merely indicate whether or not the eye is rotating, and gate the interpretation of lamellar flow as being due to a pursuit rotation or a curved path. This is consistent with the transparent motion illusion of Duffy and Wurtz (1993), which suggests that lamellar flow is used to estimate rotation when motion parallax is present. On the other hand, if the retinal flow is planar (not 3D), the rotation rate is quantitatively estimated from extraretinal signals, but with a gain of only 50%. This is consistent with the partial compensation for eye movements observed in MSTd cells with planar flow patterns (Bradley et al., 1996).

Furthermore, it appears that extraretinal signals begin to make a contribution half a second after the onset of flow (Grigo and Lappe, 1999). With simulated rotation displays shorter than 500 msec, heading toward a large frontal plane (Fig. 84.3) is judged accurately based on minimal motion parallax, whereas with longer displays heading is perceived erroneously at the fixation point. Given that fixations normally last for 300 to 500 msec, the results imply that under ordinary conditions the visual system may rely primarily on retinal flow.

Two neural models of MSTd incorporate extraretinal influences. Beintema and van den Berg (1998) assume flow templates with Gaussian tuning for combinations of radial and lamellar flow, similar to those of Perrone and Stone (1994). The model uses an extraretinal velocity signal to modulate the gain of a subset of units tuned to the corresponding rotation rate. Lappe (1998) assumes flow templates with sigmoidal tuning and uses an extraretinal velocity signal

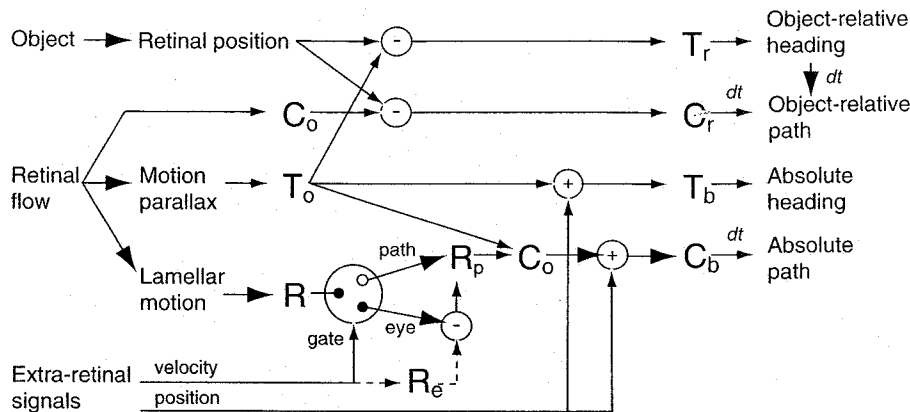


FIGURE 84.5. A heuristic summary of the flow of information in the visual system for recovering heading and path of self-motion. T , observer translation; R , total rotation; R_e , rotation attributed to eye and head pursuit; R_p , rotation attributed to path curvature; C , circular path. Subscripts o , b , and r indicate quantities in oculo-centric, body-centric, and object-relative reference frames, respectively.

to shift the tuning of individual cells so that the population response compensates fully for rotation. Given that a majority of expansion cells appear to have Gaussian-like tuning, and some evidence of gain modulation in MSTd, the first model would seem to be more plausible; on the other hand, the second model captures the observation that partial shifts in individual cells can yield full compensation in a population vector. However, both models assume that extraretinal signals provide an accurate measure of rotation rate, rather than gating the interpretation of retinal flow, and neither incorporates object-relative heading. Given the current state of knowledge, one must remain agnostic about such models, but they can help to guide further tests of MSTd.

A heuristic interpretation of the flow of information in the visual system, based on the results we have surveyed, appears in Figure 84.5. The lower part of the diagram illustrates the recovery of absolute heading and the upper part the recovery of object-relative heading. The evidence is generally consistent with the view that oculocentric translation (T_o) is determined from motion parallax and total rotation (R) from lamellar flow, either via parallel MT-MSTd pathways for differential and common motion or via compound templates in MSTd. The role of extraretinal velocity signals is largely limited to gating the total rotation R to eye and head pursuit or to path curvature (R_p), from which the instantaneous circular path (C_o) is determined. In the former case, they may provide a quantitative estimate of eye and head rotation (R_e), which is subtracted from R to estimate R_p when motion parallax is absent or fixation exceeds a half-second. To recover the absolute heading and path, extraretinal position information is needed to convert from oculocentric to body-centric frames. In contrast, objectrelative heading (T_r) is determined by merging the oculocentric heading (T_o) with an object's retinal position, bypassing the coordinate transformation. Similarly, to recover the object-relative path (C_r), the path determined from the curved flow field (C_o) is merged

with the object's position, or object-relative heading may be updated over time. Normally, the absolute and relative solutions are congruent, but during simulated rotation they are in conflict, and the object-relative solution tends to dominate.

Controlling locomotion with optic flow

We have now established that humans can perceive self-motion from optic flow under a variety of conditions and that specialized neural pathways exist to extract this information. Despite these findings, it is not a foregone conclusion that optic flow is actually used to control locomotor behavior, for other strategies are also available.

To locomote toward a stationary goal, an obvious strategy is simply to walk in the egocentric direction of the target, without using optic flow at all. For example, one could center the goal at the midline of the body and walk forward. Alternatively, optic flow from the scene could be used to steer toward a goal, using relations that are all within the visual domain. For example, one could walk so as to cancel the error between the FOE and the goal (Gibson, 1950) or between the perceived heading and the goal.

These hypotheses can be dissociated by using wedge prisms, which deflect the visual direction of the FOE from the direction of walking (Rushton et al., 1998). Thus, if participants guide walking by placing the deflecting FOE on the deflecting target, the "virtual" heading error between the FOE and the target will still be canceled, leading them to walk a straight path to the goal. But if they walk in the direction of the displaced image of the target, the virtual heading error will equal the prism deflection, and they will trace out a curved path to the goal. This is precisely what is observed with prisms in an open field, where there is minimal optic flow from fine grass texture, demonstrating that people can use egocentric direction to guide walking. On the other hand, we used a virtual reality lab to displace the FOE from

the direction of walking in a similar manner and manipulated the textured surface area in the display (Warren et al., 2001). In this setup, paths are significantly straighter and virtual heading error is reduced to near zero as optic flow and motion parallax are added to the display, consistent with an optic flow strategy. Similar improvements have also been reported with prisms as visual structure is added (Harris and Carre, 2001; Wood et al., 2000). Thus, both optic flow and egocentric direction contribute to the visual control of walking. Such redundancy provides robust locomotor control under a variety of environmental conditions.

In contrast, when walking to intercept a moving target, people rely solely on the visual direction of the target. Specifically, they walk with a direction and speed that keeps the bearing angle of the target constant, much like a sailor colliding with another boat (Fajen and Warren, 2002). This makes sense because radial flow from the whole scene is no longer informative about one's path toward a moving target.

We recently developed a dynamic theory of steering and obstacle avoidance that is based on object-relative heading with respect to goals and obstacles (Fajen et al., in press). Specifically, a goal acts like an attractor of heading, whose strength increases with its angle from the current heading and decreases with distance. In contrast, obstacles act like repellers of heading, whose strength decreases with both angle and distance. The resultant of these forces determines the current walking direction at a constant speed. The model closely fits human behavior for walking toward a goal, detouring around an obstacle, intercepting a moving target, avoiding a moving obstacle, and even predicts routes through an array of obstacles. In principle, such a model could be extended to include interactions among these basic behaviors, accounting for paths of locomotion in a complex dynamic environment.

Conclusion

We have followed optic flow through the cycle of perception and action, describing how information is generated by motion through the environment, detected to determine self-motion, and used to control behavior. Yet important questions remain unanswered. How, exactly, are translation and rotation determined from motion parallax and lamellar flow—in parallel pathways or compound templates? Can these processes account for the way moving objects bias perceived heading? How are curved paths of self-motion recovered and coded in this pathway? Precisely how do retinal and extraretinal signals interact? Are there distinct cortical representations of oculo-, head-, and body-centric heading or of object-relative heading? Is locomotion guided by perceived heading per se or by some other aspect of optic flow? And how is flow used in concert with proprioceptive and vestibular information to control locomotor behavior?

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