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2.12 Optic Flow

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Glossary

- **curl**: The local rate of rotatory flow at a point in the flow field.
- **deformation (def)**: The local rate of shear along two orthogonal axes at a point in the flow field.
- **differential motion**: Motion parallax between points at different depths within a local neighborhood of the visual field.
- **divergence (div)**: The local rate of expansion at a point in the flow field.
- **expansion**: Informally refers to a radial flow.
- **extraretinal signals**: Efferent, proprioceptive, or vestibular signals that are produced by eye or head movements.
- **focus of expansion (FOE)**: The fixed point at the center of a radial flow pattern. The divergence at the focus of expansion is zero.
- **heading**: The observer’s instantaneous direction of translation. If the observer is traveling on a straight path, the heading direction coincides with the path direction; if traveling on a curved path, the heading direction is tangent to the path.
- **lamellar flow**: A pattern of parallel or laminar flow, in which the vector directions are parallel and of equal magnitude. Sometimes called translational motion or planar motion.
- **motion parallax**: Relative motion between environmental points at different depths produced by observer translation. Local motion parallax or differential motion, is defined within a neighborhood of the visual field (~15°), global motion parallax may be distributed widely across the visual field.
- **optic array**: The pattern of light reflected from environmental surfaces to a point of observation. (More generally, the volume of light reflected from surfaces to all potential points of observation, filling the medium.)
- **optic flow**: The motion pattern produced at an eye that is moving relative to environmental surfaces. The eye may be moving with respect to stationary
surfaces, or surfaces may be moving with respect to a stationary eye.

**path** The observer’s trajectory over time.

**radial flow** A flow pattern in which the velocity vectors radiate, expand, or diverge outward from a focus of expansion.

**retinal flow** The optic flow pattern projected onto the surface of the retina. Whereas optic flow is purely radial, retinal flow can have an added rotational component due to eye rotation.

**rotary flow** A flow pattern that rotates around a fixed point. Sometimes called rotational motion. The rate of rotary flow is the curl.

**rotational component** The component of retinal flow produced by observer rotation, a solenoidal flow pattern. Observer yaw or pitch generates a lamellar flow pattern, roll or torsion about the line of sight generates a rotary flow pattern.

**self-motion** Movement of the observer. Instantaneously described as the sum of a translation and a rotation, each having a direction and a speed.

**solenoidal flow** A flow field without sources or sinks (such as a focus of expansion or contraction).

**time-to-contact** The time remaining before a moving observer hits an environmental surface (or vice versa).

**translational component** The component of retinal flow produced by observer translation, a radial flow pattern.

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2.12.1 Introduction

When an observer moves through the environment, a pattern of motion is generated at the eye known as optic flow. The term was introduced by Gibson J. J. (1950) in order to generalize Helmholtz’s notion of motion parallax to a motion field produced by the surrounding environment. The concept played a key role in the development of Gibson J. J.’s (1979) ecological approach to perception, which emphasizes the richness of information available in natural environments and the biological function of vision in guiding adaptive behavior. Optic flow provides a primary example of a higher-order variable that both specifies complex environmental relations and can reciprocally be used to control action. In particular, flow patterns contain information about the observer’s self-motion, time-to-contact with objects (Pepping, G. J. and Grealy, M. L., 2007), the motions of other objects (Burr, this volume), and the three-dimensional (3D) shape and layout of environmental surfaces (Todd, J. T., 1995; Domini, F. and Caudek, C., 2003; Siegel, R. M. this volume) and are used to control locomotion (Warren, W. H. and Fajen, B. R., 2004). In this chapter, I focus on human perception of self-motion from optic flow; the neural basis for the detection of flow patterns is reviewed in depth elsewhere (Duffy, C. J., 2004; Raffi, M. and Siegel, R. M., 2004; see Chapter Cortical Processing of Visual Motion).

2.12.2 The Optic Flow Field

Optic flow is the pattern of motion produced at an eye that is moving relative to environmental surfaces. It is commonly represented by an instantaneous velocity field, in which each vector corresponds to the optical motion of a point in the environment. (This is only a partial description because it leaves out such properties as optical acceleration, optical trajectories, dynamic occlusion, and so on.) Given that any rigid motion can be instantaneously decomposed into a translation and a rotation, it follows that the flow pattern projected on the moving retina has two corresponding components: a translational component of radial flow due to translation of the observer (Figure 1(a)) and a rotational component of solenoidal flow due to rotation of the observer (Figure 1(b)). The problem I consider is how the visual system can determine self-motion from such flow patterns.

2.12.2.1 Translational Component

Translation of the eye on a straight path generates a radial flow pattern (Figures 1(a) and 2(a)), in which the vectors radiate outward from a focus of expansion in the direction of travel or heading and converge to a focus of contraction in the opposite direction. The radial pattern formed by the directions of the vectors depends solely on the observer’s direction of travel and is independent of the distance of environmental
surfaces. Hence, it uniquely specifies the current heading direction. On the other hand, the magnitude of each vector depends on its visual angle from the focus of expansion, the observer’s speed of travel, and the distance of the corresponding point in the environment. Thus, flow magnitudes carry information about relative depth and are also correlated with the observer’s heading.

In principle, determining heading from the radial flow pattern is straightforward. Any pair of vectors can be triangulated to determine their common point of origin, and doing so for many pairs yields a reliable estimate of the focus of expansion. The flow field is thus highly redundant and supports a robust heading estimate in the presence of noise, although biases result if the focus itself is not in view. This suggests a process of spatial integration in which heading is determined by pooling over many vectors in a flow pattern.

### 2.12.2.2 Rotational Component

When the observer rotates via either an eye or head movement, the resulting retinal flow pattern is solenoidal, that is, without sources or sinks (Figure 1(b)). Specifically, yaw or pitch of the observer generates a lamellar or parallel flow pattern (Figure 2(b)), whereas roll about the line of sight generates a rotary flow pattern. The rotational component of flow is independent of distance and carries information about the observer’s rotation. In particular, the vector directions depend entirely on the axis of rotation, and hence specify the observer’s rotation direction. The vector magnitudes depend on their visual angle from the rotation axis and the speed of rotation, and hence specify the observer’s rotation rate. Spatial integration over the flow pattern would thus permit the determination of the direction and speed of observer rotation.

### 2.12.2.3 Combined Translation and Rotation

When the eye is translating, the direction of heading is specified by the radial pattern of optic flow. But the
optic flow must be detected by a moving eye in a moving head, and observer rotation alters the flow pattern on the retina. When the eye is simultaneously translating and rotating, the retinal flow pattern is the vector sum of the corresponding translational and rotational components (Figure 2(c)). A pursuit eye movement induced by fixating a point in the environment, for example, annihilates the focus of expansion in the heading direction and creates a new singularity at the fixation point, as illustrated in Figure 2(c). How, then, can the visual system disentangle the translational and rotational components of retinal flow to recover the instantaneous heading direction? This has come to be known as the rotation problem in heading perception.

It is worth noting that the flow pattern on the retina is usually radial. About 60% of the time, walkers exhibit travel gaze fixation, in which the gaze direction is fixed relative to the heading direction, without pursuit movements (Patla, A. E. and Vickers, J. N. 1997; 2003). However, the rest of the time they tend to fixate obstacles, targets on the ground, or the locomotor goal, often inducing pursuit rotations.

Fortunately, as long as the environment has 3D structure, the retinal flow contains sufficient information to solve the rotation problem in principle. Specifically, observer translation is specified by the motion parallax between points at different depths, whereas observer rotation is specified by the common lamellar motion across the visual field. But with little depth structure, as in the case of a frontal plane with a small field of view, there is little motion parallax across the display because the distance of the surface from the eye changes very little. Reprinted from Warren, W. H. and Hannon, D. J. 1990. Eye movements and optical flow. J. Opt. Soc. Am. A 7, 160. copyright 1990 by Optical Society of America.

2.12.3 Perception of Self-Motion

We now turn from the properties of the flow field to consider empirical data on perceiving self-motion.

2.12.3.1 Perception of Translational Heading

Psychophysical results demonstrate that heading can be perceived from radial optic flow patterns with an accuracy better than 1° of visual angle (Warren, W. H. et al., 1988). In such experiments, participants view random-dot displays of radial flow with either stationary or free fixation and judge the direction of self-motion. Consistent with the independence of radial flow from distance, heading accuracy is comparable with different 3D scenes, including a ground plane, a frontal plane, or a cloud of dots. It remains high when the vector magnitudes are randomized, leaving only the radial pattern, but not when vector directions are randomized (Warren, W. H. et al., 1991a). Consistent with the notion of spatial integration, heading judgments improve with the number of dots in the display (Warren, W. H. et al., 1988) and are robust to added noise in vector directions (Warren, W. H. et al., 1991a). Moreover, judgments of motion direction in displays of radial, rotary, and lamellar flow improve as the area of coherent motion increases, indicative of spatial summation over visual angles up to 72° (Burr, D. C. et al., 1998).

The psychophysical evidence suggests that there are independent neural mechanisms sensitive to radial, rotary, and lamellar flow, either at the single-cell or at the population level. Judgments of expansion in spiral flow patterns that combine radial and rotary motions are comparable to those for radial flow patterns alone (and vice versa) (Freeman, T. C. and Harris, M. G., 1992; Barraza, J. F. and Grzywacz, N. M., 2003), and the same holds for combinations of radial or rotary motion with lamellar motion (Kappers, A. M. L. et al., 1994; 1996; Te Pas, S. F. et al., 1996).
These behavioral data cohere with the results from single-cell recordings in primate visual cortex. The dorsal medial superior temporal area (MSTd) contains cells selective for expansion/contraction, rotary flow, and lamellar flow (Saito, H. et al., 1986); a majority of cells respond to two or three of these individual patterns (Duffy, C. J. and Wurtz, R. H., 1991a), and there is evidence for intermediate units tuned to spiral flow (Graziano, M. S. A. et al., 1994). Such cells have large receptive fields up to 65° in diameter, exhibit stronger responses to larger flow patterns, and are position invariant, consistent with spatial integration of local motions (Tanaka, K. and Saito, H., 1989; Duffy, C. J. and Wurtz, R. H., 1991b; Lagae, L. et al., 1994). Moreover, 90% of expansion units have receptive fields with a preferred focus of expansion (Duffy, C. J. and Wurtz, R. H., 1995; Raiguel, S. et al., 1997), and microstimulation in MSTd biases the heading judgments of macaque monkeys (Britten, K. H. and Wezel, R. J. A. v., 1998). Although some expansion cells prefer an increasing speed gradient from center to periphery (Duffy, C. J. and Wurtz, R. H., 1997), eliminating the speed gradient has a far smaller impact on a cell’s response than eliminating the radial pattern of directions (Tanaka, K. et al., 1989). These results suggest a distributed coding of the focus of expansion in MSTd, although further processing of optic flow takes place higher in the dorsal pathway, including the ventral intraparietal area (VIP), area 7a, and the superior temporal polysensory area (STPa).

In sum, the evidence indicates that the direction of heading can be accurately perceived from radial flow patterns, and neural substrates for the extraction of radial, rotary, and lamellar flow appear to be present in the primate visual system.

2.12.3.2 Perception of Rotation

The psychophysical data on the perception of observer rotation come largely from the literature on circular (yaw) vection, a visual illusion of self-motion produced by a striped drum rotating about a stationary observer. As expected from the flow field analysis, the perceived speed of complete vection closely corresponds to that of the visual display over a wide range, up to a saturation velocity of about 120° s⁻¹ (Brandt, T. et al., 1973). Surprisingly, however, perceived speed also increases with the perceived distance of the display (Wist, E. R. et al., 1975), contrary to the independence of the flow magnitude from distance. However, yaw rotation may be partially perceived as lateral translation of the observer, due to the similarity of the flow patterns generated with a 2D surface; tests of a 3D display with motion parallax are required. To my knowledge, there are no data on the perceived direction (axis) of self-rotation.

It is suggestive that most MSTd cells respond to lamellar motion, with large receptive fields, direction selectivity, and broad tuning to the overall speed of motion (Saito, H. et al., 1986; Tanaka, K. and Saito, H., 1989; Orban, G. A. et al., 1995). Moreover, many of these cells also encode pursuit eye movements, with a preferred pursuit direction that is on average opposite the preferred flow direction (Komatsu, H. and Wurtz, R. H., 1988). These characteristics are appropriate for the detection of flow patterns produced by eye or head rotation.

2.12.3.3 Decomposing Translation and Rotation

When one walks on a straight path while making a pursuit eye movement, the eye is simultaneously translating and rotating, and the retinal flow pattern corresponds to the sum of these two components (Figure 2). How might the visual system decompose this complex flow pattern to recover the observer’s instantaneous heading and self-rotation? There are two general approaches to this problem, one relying on the information in retinal flow and the other on extraretinal signals about eye and head rotation.

2.12.3.4 Retinal Flow Theories

It has been shown formally that the retinal flow pattern for a 3D scene contains sufficient information to recover the translational heading during rotation. This is possible in principle because a rotation simply adds a constant to the flow field, leaving the motion parallax intact. There are roughly five classes of retinal flow theories, which will be briefly described: discrete, differential, subtractive, local motion parallax, and template models (see Hildreth, E. C. and Royden, C. S., 1998; Warren, W. H., 1998; Lappe, M. et al., 1999 for reviews).

Initially, several discrete models proved that observer translation and rotation can be computed from the motions of a minimum number of points in two successive images (Prazdny, K., 1980; Longuet-Higgins, H. C., 1981; Tsai, R. Y. and Huang, T. S., 1981). At the same time, a class of differential models showed that self-motion and surface slant can be determined from spatial derivatives of the flow field.
such as divergence, curl, and deformation, as well as lamellar motion (Koenderink, J. J. and van Doorn, A. J., 1975; Longuet-Higgins, H. C. and Prazdny, K., 1980; Koenderink, J. J. and van Doorn, A. J., 1981; Waxman, A. M. and Ullman, S., 1985). However, these theories rely on precise measurements of a few points and are highly vulnerable to noise, or assume surface smoothness, casting doubt on their biological plausibility (see also Kappers, A. M. L. et al., 1996).

A third class of theories first estimates the rotational component from the lamellar flow, and then subtracts it from the flow pattern to determine the translational component (Perrone, J. A., 1992). Koenderink J. J. (1986) noted that observer rotation during translation can be estimated by independently integrating the global flow about three orthogonal axes, and there is evidence for such a system in the rabbit (Simpson, J. I. et al., 1981).

A complementary class of theories determines the translational component from local motion parallax, also known as differential motion (Longuet-Higgins, H. C. and Prazdny, K., 1980; Rieger, J. H. and Lawton, D. T., 1985; Lappe, M. and Rauschecker, J. P., 1993; Cutting, J. E., 1996; Royden, C. S. 1997). Differential motion is due to depth differences within a local neighborhood in the flow field and can be represented by a difference vector. Remarkably, the set of difference vectors once again forms a radial pattern centered on the heading and is invariant to rotation. The rotation problem can thus be solved quite elegantly if there is sufficient 3D structure in the scene.

Finally, a fifth class is based on templates for the set of flow patterns generated by possible combinations of observer translation and rotation (Perrone, J. A. and Stone, L. S., 1994; Beintema, J. A. and van den Berg, A. V., 1998; Perrone, J. A. and Stone, L. S., 1998). Each such template is selective for a complex motion pattern, rather than for an elementary flow component. Due to depth variation in the environment, however, the space of possible flow patterns is very large and must be constrained, for example, by assuming fixation of a point attached to the scene. These analyses demonstrate that it is theoretically possible to determine the observer’s translation and rotation from the retinal flow pattern alone.

2.12.3.5 Extraretinal Theories

In contrast, the extraretinal approach proposes that efferent or proprioceptive signals about the rotational velocity of the eye and head are used to estimate the observer’s rotation (Royden, C. S. et al., 1994; Banks, M. S. et al., 1996); interestingly, vestibular signals seem not to play a role (Crowell, J. A. et al., 1998). In principle, the rotational component can then be subtracted from the retinal flow pattern in order to determine the instantaneous translational heading.

One possible implementation uses extraretinal velocity signals to subtract the rotational component at the level of MSTd, thereby shifting the preferred focus of expansion within the retinal receptive field. This implies head-centric expansion cells in MSTd that fully compensate for eye rotation. A related model realizes a least-squares solution to the rotation problem in the connection weights from MT to MSTd, augmented by extraretinal signals that modulate MSTd responses (Lappe, M., 1998). The model implies sigmoidal tuning curves and a population code for heading at the level of MSTd. Alternatively, MSTd cells might serve as templates for combinations of radial and lamellar flow, with extraretinal velocity signals modulating their response gain to create a heading map in a separate neural layer (Beintema, J. A. and van den Berg, A. V., 1998). This implies the existence of gain fields and head-centric expansion cells elsewhere in the dorsal pathway.

A fourth possibility is a recurrent basis function network, with separate input layers that code oculocentric flow signals, head-centric vestibular signals, and extraretinal eye position signals, which are recurrently connected to a multisensory layer such as MSTd (Pouget, A. et al., 2002; Fetsch, C. R. et al., 2007). This model implies gain fields and a continuum of intermediate reference frames in MSTd, without convergence on common head-centric units.

2.12.3.6 Perception of Heading During Rotation

The empirical question at hand is whether humans can in fact perceive their instantaneous heading during an eye rotation on the basis of retinal flow alone, or whether extraretinal signals are necessary. The evidence, though still controversial, points to the conclusion that the visual system exploits both types of solutions.

2.12.3.7 Simulated Rotation

The rotation problem has been investigated using displays that simulate the retinal flow corresponding to a pursuit rotation, while the eye is actually
stationary (see Figure 2(c)); any extraretinal signal thus indicates zero rotation. Initially, Warren W. H. and Hannon D. J. (1988; 1990) reported heading thresholds better than 1.5° during both simulated and real eye rotation (for rotation rates <1° s⁻¹), as long as there was 3D structure in the scene, consistent with retinal flow theories based on motion parallax. With a frontal plane of dots, on the other hand (Figure 3), heading judgments were only accurate during real eye movements, consistent with extraretinal theories. Yet Grigo A. and Lappe M. (1999) reported accurate judgments during simulated rotation with a larger field of view, presumably due to global motion parallax from the periphery (Grigo, A. and Lappe, M., 1999). Subsequent research also supported some version of a retinal flow theory (Cutting, J. E. et al., 1992; van den Berg, A. V. 1993; 1996; Stone, L. S. and Perrone, J. A., 1997; Wang, R. F. and Cutting, J. E., 1999).

However, when Banks, M. S. and his colleagues (Royden, C. S. et al., 1992; 1994; Banks, M. S. et al., 1996) tested higher rotation rates (1–5 s⁻¹), they found large heading errors of up to 15° in the simulated rotation condition, contrary to retinal flow theories. Whether the visual system can determine the direction of heading from retinal flow was thus cast into doubt.

2.12.3.8 The Path of Self-Motion

There is, however, a known ambiguity in the retinal flow: the same instantaneous velocity field can be produced by translation on a straight path plus a rotation, or by travel on a circular path (Figure 4). The retinal velocity field by itself is thus insufficient to distinguish straight and curved paths of self-motion, which is known as the path ambiguity. (Theoretically, the ambiguity can be resolved by considering accelerative components of the flow or element trajectories over time, but the evidence suggests that the visual system is not sufficiently sensitive to these properties (Warren, W. H. et al., 1991a; Ehrlich, S. M. et al., 1998; Paolini, M. et al., 2000).) Although the simulated rotation paradigm was intended to assess the perception of instantaneous heading (the tangent to the path at any moment), participants often reported seeing a curved path of self-motion, and their heading errors were consistent with this report (Royden, C. S., 1994). It thus appears that errors during simulated rotation were likely due to the path ambiguity, together with a tendency to judge the path of self-motion instead of the instantaneous heading, rather than evidence of the visual system’s inability to decompose translation and rotation.

If the retinal flow is ambiguous, how might the visual system determine the path of self-motion? On an extraretinal approach (Banks, M. S. et al., 1996), velocity signals can be used to subtract eye and head rotation from the retinal flow field; if the residual flow pattern has a rotational component, it is attributed to a curved path. However, this approach assumes accurate extraretinal signals, whereas their gain is believed to be significantly less than one (Wertheim, A. H., 1987). Moreover, the residual flow pattern may still need to be decomposed into translational and rotational components in order to estimate the curvature of that path (Ehrlich, S. M. et al., 1998). On the other hand, once the path ambiguity is resolved, it is possible that the current path may be determined directly from the curved optic flow pattern (Lee, D. N. and Lishman, R., 1977; Warren, W. H. et al., 1991b; Kim, N.-G. and Turvey, M. T., 1998).

Alternatively, the path ambiguity might be resolved by determining the object-relative heading, that is, heading, with respect to reference objects in the environment. (Li, L. and Warren, W. H., 2000). Specifically, if the instantaneous heading remains fixed relative to objects in the scene over time, then the observer is on a straight path, whereas if the heading drifts over reference objects, then the observer is on a curved path, and rate of drift corresponds to path curvature. Most previous research used sparse random-dot displays without reference objects that could be tracked over time. But when one or more distinct objects are added to a display containing textured surfaces, path errors remain below 4° (at 7° s⁻¹) (Cutting, J. E. et al., 1997; Li, L. and Warren,
W. H., 2000). This is also the case for active steering to a target during simulated rotation (Li, L. and Warren, W. H., 2002). Thus, with distinct reference objects and motion parallax from textured surfaces, the retinal flow solution tends to dominate the extra-retinal solution.

Nevertheless, simulated rotation is a cue conflict condition, and hence features of the display or task can bias the observer toward one path or the other. Extraretinal signals indicate that the eye is not rotating, so the retinal flow pattern indicates the observer is on a curved path; yet the object-relative heading remains fixed in the scene, indicating that the observer must be on a straight path. Consistent with this analysis, when participants are told they are traveling on a straight path, errors remain below $4^\circ$ (at $5^\circ \text{s}^{-1}$), whereas when they are told they are on a curved path, errors rise to $12^\circ$ (Li, L. and Warren, W. H., 2004). Thus, the visual system has the capacity to recover observer translation from the retinal flow alone.

In sum, results from the simulated rotation paradigm indicate that both extraretinal and retinal flow solutions contribute to the perception of self-motion.

### 2.12.3.9 The Optic Flow Illusion

A second paradigm that bears on the decomposition of retinal flow is known as the optic flow illusion (Duffy, C. J. and Wurtz, R. H., 1993). When a transparent plane of laterally moving dots is superimposed on a plane of radially moving dots (Figure 5), the perceived location of the focus of expansion shifts in the direction of the lateral motion. This phenomenon suggests that the visual system uses the global lamellar flow to estimate eye rotation and compensates by shifting the perceived focus of expansion in the opposite direction (Duffy, C. J. and Wurtz, R. H., 1993; Lappe, M. and Rauschecker, J. P., 1995; Pack, C. and Mingolla, E., 1998).

However, the illusion can also be explained by motion-opponent operators that extract the local differential motion between the lamellar and radial flow patterns (Royden, C. S. and Conti, D. M., 2003). Such operators could be the basis for recovering heading from local motion parallax (Royden, C. S., 1997), and also account for biases in perceived heading induced by a moving object in the scene (Warren, W. H. and Saunders, J. A., 1995; Royden, C. S. and Hildreth, E. C., 1996; Royden, C. S., 2002). When local parallax is eliminated by presenting nonoverlapping flow patterns, the focus of expansion shifts only 17% as...
far, but nonetheless a residual illusion persists (Duijnhouwer, J. et al., 2006). It thus appears that both local motion parallax and global lamellar mechanisms are involved in decomposing the retinal flow. The lamellar motion might be extracted by large-field lamellar cells or by motion-opponent units with large surrounds.

2.12.3.10 Extraretinal Signals

The simulated rotation paradigm demonstrated that extraretinal signals contribute to the estimate of observer rotation. But work by Crowell J. A. and Anderson R. A. (2001) indicates that they do so in a particular way. When the retinal flow corresponds to a 3D scene (e.g., contains motion parallax), the rotational component is determined solely from the lamellar flow. Extraretinal signals merely indicate whether or not the eye is moving and serve to gate the interpretation of the lamellar flow as either being due to an eye rotation or to a curved path of self-motion. When the retinal flow does not contain motion parallax, observer rotation is determined from extraretinal signals, but is underestimated by nearly 50%. This implies that full pursuit compensation must also depend on the lamellar flow.

Moreover, extraretinal signals only begin to play a role 500 ms after the onset of flow, prior to which heading judgments are based solely on the retinal flow (Grigo, A. and Lappe, M., 1999). Given that fixation duration is normally 300–500 ms, this implies that ordinarily the visual system determines heading primarily from retinal flow.

2.12.4 Toward an Integrated View

2.12.4.1 Functional Level

The picture of self-motion perception that emerges from the psychophysical literature looks something like the following. First, observer translation is determined from motion parallax in the retinal flow field, which depends on 3D structure in the scene. The visual system appears to extract both local differential motion and global motion parallax, and this information seems sufficient to recover the instantaneous direction of heading.

Second, observer rotation is determined from the common lamellar motion in the retinal flow. The visual system appears to extract large-field lamellar flow that corresponds to eye rotation. This rotation estimate is subtracted from the retinal flow to contribute to the recovery of the translational component, as evidenced by the residual optic flow illusion.

Third, extraretinal signals similarly contribute to the recovery of observer translation, but in a limited way. When the retinal flow contains motion parallax, the rotational component is determined from lamellar flow, and extraretinal signals merely specify whether it should be attributed to eye rotation or a curved path. In the absence of motion parallax, the rotational component is estimated from extraretinal signals, but with low gain and only after 500 ms.

Finally, the path of self-motion appears to be based on the object-relative heading over time. A heading direction that is fixed in the scene specifies a straight path, whereas a heading that shifts with respect to environmental objects specifies a curved path.

2.12.4.2 Neural Level

The neural support for these functions remains contested, given that evidence can be found for competing theories. Consistent with local motion parallax theories, a majority of cells in area MT possess bilateral motion-opponent receptive fields (Allman, J. et al., 1985; Xiao, D.-K. et al., 1997) and project to MSTd. Expansion cells in MSTd could detect the radial pattern of difference vectors, and their response is enhanced when motion parallax is added to a radial flow display (Upadhyay, U. D. et al., 2000). On the other hand, consistent with template theories, many MSTd cells respond to combinations of radial, rotary, and/or lamellar flow rather than constituting a simple heading map.

Extraretinal theories gain support from the finding that the preferred focus of expansion in most MSTd cells shifts within the retinal receptive field during a pursuit eye movement, partially compensating for the pursuit (Bradley, D. C. et al., 1996; Shenoy, K. V. et al., 1999; 2002; Lee, B. et al., 2007). Such findings appear to be consistent with a heading map in MSTd. However, the shifts undercompensate for pursuit, although full compensation might occur with motion parallax in the display. Nevertheless, the population response seems to exhibit full pursuit compensation (Page, W. K. and Duffy, C. J., 1999), consistent with Lappe M.’s (1998) model. Alternatively, these partial shifts can also be interpreted as evidence of intermediate oculocentric and head-centric reference frames in MSTd, without convergence on head-centric units, consistent with a recurrent basis function network (Fetsch, C. R. et al., 2007).
But recently, head-centric expansion cells have been identified in primate area VIP that exhibit full pursuit compensation with motion parallax in the display (Zhang, T. et al., 2004). This is consistent both with an extraretinal contribution and with determining rotation from lamellar flow in 3D displays. Such a VIP heading map is expected from the gain field model of pursuit compensation (Beintema, J. A. and van den Berg, A. V., 1998; van den Berg, A. V. and Beintema, J. A., 2000), and gain modulation of flow responses has been observed in MSTd and area 7a (Bremmer, S. et al., 1997; Read, H. L. and Siegel, R. M., 1997; Shenoy, K. V. et al., 1999).

Finally, neurons in area STPa respond to both optic flow and object boundaries in their receptive fields (Anderson, K. C. and Siegel, R. M., 1999). This suggests a possible site for the detection of object-relative heading.

### 2.12.4.3 Conclusion

In sum, current evidence indicates that the visual system exploits redundant information for robust perception of self-motion. Translational heading is determined from local and global motion parallax in the retinal flow pattern, whereas observer rotation is determined from lamellar motion and extraretinal signals and contributes to the estimate of instantaneous translation. The path of self-motion may be determined from the heading relative to environmental objects over time. These functions are carried out in a distributed dorsal network that integrates information in a head-centric heading map. Precisely how they are implemented across multiple cortical areas is a matter of ongoing investigation.

### References


