14. From Optic Flow to Laws of Control

William H. Warren¹ and Brett R. Fajen²

¹ Dept. of Cognitive & Linguistic Sciences Brown University, Providence, Rhode Island, USA

² Dept. of Cognitive Science Rensselaer Polytechnic Institute, Troy, New York, USA

1 INTRODUCTION

It is now established beyond a reasonable doubt that people can perceive self-motion from optic flow with sufficient accuracy to guide their locomotion. In particular, the direction of self-motion, or *heading*, can be judged quite accurately under a variety of conditions. However, as pointed out by Nakayama (1994), it remains controversial as to whether optic flow is actually used to control locomotor behavior. The aim of this chapter is to move beyond the perception of optic flow per se to the question of how a variety of information is used to control human locomotion on foot. We offer an interim report on an ongoing research program that seeks to determine the laws of control for steering and obstacle avoidance in a complex, dynamic environment.

2 PERCEPTION OF HEADING FROM OPTIC FLOW

Cutting and colleagues (1992) estimated that an accuracy of 1° to 3° of visual angle is needed to guide ordinary locomotor behavior such as running and skiing. In a series of psychophysical experiments over the last 15 years, it has been shown that one's current heading or future path can be judged with this level of accuracy under a wide range of environmental and viewing conditions (for recent reviews see Lappe et al., 1999; Warren, in press). For example, heading accuracy is on the order of 1° in a variety of environments (ground planes, frontal planes, 3-D clouds, realistic 3-D worlds); with dense, sparse, discontinuous, or noisy flow fields; and on straight or circular paths of

self-motion. For purely translational movements of the observer, there is consistent evidence that the visual system determines heading from the radial pattern of optic flow, in which the *focus of expansion* corresponds to one's current heading direction.

When the eye is simultaneously rotating – during a pursuit eye movement, for example – one can also recover the instantaneous heading or the path over time. After more than a decade of controversy over how the visual system handles this rotation problem (Banks et al., 1996; Royden et al., 1992, 1994; Stone & Perrone, 1997; van den Berg, 1992, 1996; Warren & Hannon, 1988; 1990), it now appears that both information in the retinal flow pattern and extra-retinal signals about eye rotation contribute to heading and path perception; for a detailed account see Warren (in press). From the retinal flow, the observer's translation in a retinal reference frame is specified by the pattern of differential motion (motion parallax) between points at different depths (Rieger & Lawton, 1985); in particular, differential motion goes to zero in the direction of heading. The observer's rotation is specified by the common lamellar motion (parallel flow) across the visual field (Perrone, 1992). Consequently, one's *object-relative heading* – the direction of heading with respect to objects that are also given in a retinal reference frame - is specified by the retinal flow pattern. The path through the environment may thus be determined from the sequence of such headings over time. In contrast, one's absolute heading in space would seem to require extra-retinal information about eye and head position.

We have recently found that, with displays containing dense motion parallax and distinct objects, both path judgments and active joystick steering are reasonably accurate during simulated rotation (Li & Warren, 2000, 2002). Such simulated rotation displays place retinal flow information specifying heading during rotation in conflict with extra-retinal signals specifying the absence of eye rotation. Yet errors remain below 4° at simulated rotation rates up to 7 deg/s. This demonstrates that extra-retinal signals are not necessary for recovering one's object-relative path. At the same time, even without dense parallax and distinct objects, path judgments during active pursuit eye movements remain accurate, indicating that extra-retinal signals also contribute.

New evidence suggests that the role of extra-retinal signals is not to provide a quantitative estimate of eye rotation (Crowell & Andersen, 2001). If the retinal flow corresponds to a 3-D scene, extra-retinal signals merely act to gate the interpretation of lamellar motion as being due to a pursuit eye movement or a curved path of self-motion. If the retinal flow corresponds to a 2-D scene, they are used to estimate the rotation rate directly, but with a gain of only 50%. Thus, a reasonable interpretation is that object-relative heading in natural 3-D environments can be recovered from the retinal flow pattern, with an assist from extra-retinal signals in determining whether the lamellar

flow is due to an eye rotation or a curved path (Warren, in press). As we shall see below, object-relative heading is precisely the sort of information that would be useful to control locomotion with respect to goals and obstacles.

3 CONTROL OF LOCOMOTION FROM OPTIC FLOW

The fact that people can accurately perceive heading from optic flow, and that specialized neural pathways exist to extract this information (Duffy, in press), would seem to imply that optic flow must be good for something in everyday behavior. But it is not a foregone conclusion that optic flow in general, or perceived heading in particular, is actually used to guide human locomotion (Wann & Land, 2000). Gibson (1958/1998; Warren, 1998) originally proposed a set of "formulae" by which optic flow could be used to steer toward goals, avoid obstacles, and chase or escape moving objects. But for any such locomotor task, a number of alternative strategies are also available. The challenge is to formally model and experimentally test the laws of control that actually govern human locomotion. We argue that such control laws must take into account not only visual information, but also the organization of the action system and the physics of the environment.

3.1 Laws of Control

A control law is generally considered to be a mapping from task-specific informational variable(s) to action variable(s) that describe observed behavior.

$$a = f(i) \tag{1}$$

If regularities in behavior can be identified at this level of abstraction, it suggests that there are systematic dependencies of action on information, presumably attributable to the laws of ecological optics. In some instances, these control principles may be quite general, spanning species from insects to humans (Duchon & Warren, 2002; Lee, van der Weel et al., 1992; Srinivasan, 1998; Wang & Frost, 1992). But how, exactly, are we to write such laws of control? There is little agreement in the literature, so let us consider several possible formulations.

First, control laws may be written in a *kinematic form*. This is a function that relates an informational variable directly to a kinematic movement variable such as limb trajectory, velocity, or timing

...

$$\dot{a} = f(i) \tag{2}$$

In this vein, Lee (1980, 1985) proposed that the onset of a movement to avoid an approaching object might be triggered at a critical value of the optical variable *tau*, which specifies the first-order time-to-contact. More recently, Lee (1998) suggested that the trajectory of a movement could be determined by the continuous coupling of two *tau* functions relating, say, the rate of closure of the distance to the target and the rate of closure of the angle of approach. Such a formulation provides a summary description of the relation between information and behavior, with the advantage that its terms are directly observable. However, it assumes that the organization of the action system doesn't contribute to the form of the behavior, and leaves out of account how the required movement is generated.

Second, control laws might take a *kinetic form*, a mapping from information to the effector forces that produce movement (Warren, 1988). Specifically, this would be a function that relates an informational variable to a force-related variable

$$F = f(i) \tag{3}$$

For example, Warren, Young, & Lee (1986) proposed that step length during running may be controlled by using the difference in time-to-contact between the next two footholds to regulate the vertical impulse of the push-off, given a constant body mass. However, this description still leaves out the action system and how it generates such forces.

We suggest that control laws be written in a *dynamic form*. The way that information can influence movement is by means of modulating the dynamics of the action system, which in turn generates effector forces. On this view, behavior is a function of the current state of the action system together with information that regulates the control variables of the system (Warren, 2002). This can be expressed functionally as a dynamical system

$$\dot{a} = \Psi(a, i) \tag{4}$$

The control law does not specify the kinematics of movement per se, but rather specifies an *attractor* for the action system. Such a fixed point or stable orbit corresponds to the goal of the intended action, and is converted into joint torques and limb movements given the properties of the musculo-skeletal system. The net result is a force exerted by effectors in the environment.

The difficulty here is that control relations between informational variables and control variables are not directly observable, but must be inferred from behavior. Thus, we will begin at a higher level of analysis with a description of the time-evolution of observable behavior, which we will call the *behavioral dynamics*. Then we may be able to infer *control laws* at a lower level that generate this behavioral outcome. Control laws thus

characterize how information about the environment acts to modulate the control variables of a dynamical system, leading to adaptive behavior. In what follows, we will develop these concepts beginning with the information that is used to control locomotion, followed by our recent research on the behavioral dynamics of locomotion, and finally considering how we might derive control laws from these results.

3.2 Strategies for Steering to a Goal

A primary question is whether optic flow is actually used to guide human locomotion. Consider the most fundamental case of steering to a stationary goal. An optic flow strategy supposes that one would walk so as to create a flow pattern corresponding to self-motion toward the target. But there is a simple alternative: one could also walk in the perceived egocentric direction of the target, without relying on optic flow at all.

Normally these two strategies are redundant and would yield similar, successful behavior. One might expect that biology take advantage of such redundancy to achieve robust locomotor control under a range of conditions. For example, in a visually structured environment, optic flow allows for heading judgments that are an order of magnitude more precise than those based on proprioceptive information about the direction of walking (Telford et al., 1995). This advantage could be due to the fact that object-relative heading is defined within a retinal reference frame, avoiding coordinate transformations that may accumulate error between eye, head, body, and effector frames. But when traveling at night or in fog, optic flow is unavailable and the system can fall back on egocentric direction.

The optic flow and egocentric direction strategies are actually two broad classes that can be broken down into more specific hypotheses. For convenience of analysis, let us define the physical heading by the angle ϕ between the current direction of locomotion and an arbitrary reference axis (see Figure 1). We also define the direction of a goal by the angle ψ_g with respect to the same reference axis. The object-relative heading, or heading error, is thus $\beta = \phi - \psi_g$, and the simplest definition of steering to the goal is to bring β to zero. Consider some possible flow strategies for adopting a straight path to a target.

• *Heading hypothesis*. Gibson (1958/1998, 1979) originally proposed that to aim locomotion at a goal, one should keep the focus of expansion near the goal. This formulation applies to the case of observer translation, but as we have seen it is complicated by the rotation problem, as well as by moving objects (Saunders & Warren, 1996). Thus, a more general



Figure 1. Definition of variables

version of the same principle is to *keep one's perceived heading near the* goal (Warren, 1998). Note that the heading may be specified by the focus of expansion in the case of pure observer translation, or more generally by the direction in which motion parallax goes to zero. The required turning angle is specified by the object-relative heading (β); the turning rate has been discussed by Lee (1998) and Fajen (2001).

• *Raw retinal flow hypothesis.* Other steering strategies do not require that heading be explicitly determined, but are based on the "raw retinal flow" when fixating the goal. In this hypothesis, the observer would *fixate the goal and steer so as to make the retinal flow pattern radial or symmetrical.* If the goal is fixated at eye level, the required steering adjustments could be determined from the curvature of the flow in the ground plane: if the flow curves to the right, one is heading to the left of fixation, so steer rightward, and vice versa. Alternatively, steering adjustments might be derived from Cutting, et al.'s (1992) concept of differential motion parallax. Environmental objects that are closer than the fixated goal appear to move across the line of sight opposite the heading direction. If such motion is rightward, and vice versa.

One can also formulate specific versions of an egocentric direction strategy, based on information about the visual direction of the target with respect to the body.

- Locomotor axis hypothesis. The first alternative is directly analogous to the heading hypothesis above, except that the current direction of locomotion is specified by proprioception, which we will call the body's locomotor axis. Specifically, to walk to a goal, *keep the felt locomotor* axis pointing in the direction of the goal. The heading error β is specified by the angle between the current locomotor axis and the visual direction to the goal. Due to their parallel form, the heading and locomotor axis strategies provide straightforward redundancy in locomotor control. However, this hypothesis relies on a unique relation between effector proprioception and the direction of movement in terrestrial locomotion, which does not hold for aerial or aquatic environments (Gibson, 1966).
- Thrust hypothesis. A closely related strategy is to perceive the egocentric direction of the goal and apply thrust force in the opposite direction. Whereas the preceding hypothesis was based on the relation between the goal and proprioception, this hypothesis is based on the relation between the goal and motor commands. Thus, it can be used to guide the initiation of walking toward the goal from a standstill. Note that the axis of thrust need not be aligned with the anterior-posterior (AP) axis of the body, for the observer can "crab" sideways. This hypothesis relies on a unique relation between the direction of force application and the resulting body displacement in terrestrial locomotion.
- *Centering hypothesis*. A special case of the locomotor axis hypothesis assumes that the eyes, head, and AP axis tend to align with the locomotor axis during walking. To walk to a goal, the observer can thus *fixate the goal, center it at the midline of the body and walk forward*. If one's gaze and head initially deviate from the AP and locomotor axes, they tend to come into alignment, analogous to the uncoiling of a twisted spring. This hypothesis is consistent with the folk wisdom that you should look in the direction you want to go and not at obstacles you want to avoid.
- *Target drift hypothesis.* Finally, one could walk so as to *cancel target drift, keeping the goal in a constant egocentric direction.* This strategy actually takes advantage of a local feature of the optic flow; that the only fixed point in the flow field ahead is at the focus of expansion. Thus, if one is heading toward the target, its optical drift is zero and hence its egocentric direction remains constant. Otherwise, it will drift away from the current heading point, providing a basis for steering adjustments.

A number of other hypotheses have been suggested that yield a curved path to the goal (Kim & Turvey, 1999; Lee, 1998; Wann & Land 2000; Wann

283

& Swapp, 2000). However, we will show that during actual walking people do not adopt continuously curved paths to a goal, but rather turn onto a straight path. There may be situations in which a curved path is called for, such as driving around a bend, but such lane-following tasks appear to involve special strategies (Beal & Loomis, 1996; Land, 1998; Land & Lee, 1994). Thus, we will not pursue the curved path hypotheses here.

In experiments on joystick steering, with simulated rotation corresponding to fixation of the target, participants are able to steer accurately as long as motion parallax is present in the display (Frey & Owen, 1999; Rushton et al., 1999). By itself, this finding does not differentiate the heading and raw retinal flow hypotheses, because steering could be achieved either by aligning the perceived heading on the target or by making the flow symmetric around the target. But participants can steer straight paths toward a target even with simulated fixation elsewhere in the display (Li & Warren, 2002), an ability that cannot be accounted for by the raw retinal flow hypothesis. The pattern of results for active steering is quite similar to that for heading judgments (Li & Warren, 2000), consistent with the heading hypothesis. Moreover, a moving object biases both heading judgments and joystick steering in precisely the same way (Royden & Hildreth, 1996; Warren & Saunders, 1995), consistent with the idea that locomotor control is based on perceived heading. The preliminary evidence thus seems more in line with a heading strategy than one based on raw retinal flow with a fixated target.

However, experiments on joystick steering cannot test egocentric direction strategies. With a joystick and a computer monitor, the locomotor axis and direction of thrust are not specified, and the mapping between joystick movement and the direction of locomotion in the display must be learned. To test locomotor strategies, therefore, we must turn to experiments on the hoof.

3.3 Is Optic Flow Used to Walk to a Goal?

The first cut through the panoply of hypotheses is to compare the two broad classes of optic flow and egocentric direction strategies. However, because these two strategies are normally redundant and predict the same behavior, they must be dissociated by varying the optic flow independently of the locomotor axis. We originally attempted this in a "virtual treadmill" apparatus, by manipulating the optic flow on a projection screen for a participant walking on a treadmill (Warren & Kay, 1997). However, the presence of the screen and the confines of the treadmill raised the possibility of artifactual strategies. We subsequently transferred the experiments to the large-scale Virtual Environment Navigation Lab (VENLab), a 12 m by 12 m room equipped with a sonic/inertial head-tracking system in the ceiling. Participants can walk freely while wearing a head-mounted display (60° H x 40° V) and be immersed in a virtual environment.

At the same time, Rushton et al. (1998) arrived at a low-tech solution wedge prisms. Suppose that a participant wearing displacing prisms is walking directly toward a target, which is 10 m away on a grass lawn. The prisms displace both the target and the optic flow by 16° from the direction of walking (to the right, say), such that the focus of expansion remains on the target. Thus, if participants rely on the optic flow, they should keep the flow centered on the target (virtual heading error $= 0^{\circ}$) and continue walking on a straight path. However, if they rely on the egocentric direction of the target, they should walk 16° to the right, toward the displaced image of the target. This shifts the focus of expansion to the right of the target (virtual heading error $= 16^{\circ}$), causing the target to drift slowly to the left in the visual field. As the participant continues to turn toward the drifting image of the target, they will trace out a curved path. And this is exactly what Rushton, et al. (1998) reported: participants followed curved paths to the target, with virtual heading errors close to 16°. These results are wholly consistent with an egocentric direction strategy, showing no influence of optic flow on walking.

However, the optic flow available in this experiment was rather minimal, defined only by the fine texture of the grass on the ground plane. In addition, prisms introduce blur and optical distortion that warps the flow pattern. These effects may have reduced reliance on the optic flow, resulting in the dominance of an egocentric direction strategy.

In the VENLab, we manipulated the area and magnitude of optic flow in the display by varying the visual structure of the environment (Warren et al., 2001). We created a similar displacement by offsetting the focus of expansion in the HMD 10° to the right or left (randomly) of the participant's actual direction of walking. The predictions are the same: if participants rely on optic flow, they should keep the focus of expansion aligned with the goal (a virtual heading error of 0°), resulting in a straight path; whereas if they rely on egocentric direction, they should keep the locomotor axis aligned with the goal (a virtual heading error of 10°), resulting in a curved path.

With an isolated target line on a black background, there was little optic flow, and participants closely followed the curved path predicted by the egocentric direction strategy (Figure 2a). Informal observations suggest that people tended to align their head and AP axis with the target and walk forward, as suggested by the centering hypothesis. However, as a textured ground plane (Figure 2b) and a textured ceiling and frontal wall (Figure 2c) were added, paths became significantly straighter and heading error significantly decreased. Finally, when an array of textured posts was added,



Figure 2. Walking to a target in four virtual environments that vary the amount of optic flow. Center column: mean path in the virtual world. Right column: mean virtual heading error as a function of distance from the start. Curves indicate between-subject SE (...), egocentric direction prediction (+++), optic flow prediction ($_$. $_$). [From Warren, et al., 2001; used by permission.]

creating salient motion parallax, heading errors decreased to about 2° (Figure 2-D). Participants started walking in the egocentric direction of the target, but once the optic flow became available their paths quickly straightened out and heading error dropped. In this case, observations suggest that they tended to align their head and AP axis – but not their locomotor axis – in the visual direction of the target, so that they "crabbed" slightly sideways. These results strongly indicate that both egocentric direction and optic flow information contribute to the control of walking, but the latter increasingly dominates as more flow becomes available.

We modeled this as an additive relation in a simple dynamical control law. Specifically, the rate of change in heading $(\dot{\phi})$ is a function of the current heading error, which is given by a linear combination of egocentric direction and optic flow

$$\dot{\phi} = -k \Big[\left(\phi_{ego} - \psi_g \right) + wv \Big(\phi_{flow} - \psi_g \Big) \Big]$$
⁽⁵⁾

The coefficient k is a turning rate constant. The current heading error is redundantly specified by the egocentric direction of the goal with respect to the locomotor axis $(\phi_{loco} - \psi_g)$, and by the visual angle between the goal and the heading given by optic flow $(\phi_{flow} - \psi_g)$. Finally, the flow contribution is weighted by the observer's velocity v, which influences the flow rate, and by w, a measure of the visual area and magnitude of optic flow due to environmental structure. Thus, if the observer is walking slowly or there is little visual structure, the flow contribution will be minimal. We simulated the initiation of walking by increasing v from 0 to 1 m/s as a logistic function of time over the first 2 sec. $(\phi_{loco} - \psi_g = 0)$; the initial direction of walking was toward the goal. Simulations in which w ranged from 0 to 6 show a pattern of results similar to the human time series of heading error in Figure 2.

Why do our results differ from those of Rushton, et al. (1998)? Minimal flow from the grass may be part of the answer. To test the role of the prisms, we had participants wear wedge prisms inside our HMD while they walked in the same four environments. The prisms displaced the optic flow by 10° , always to the right, which we compared with a computed offset of the optic flow to the right. The influence of the flow was significantly reduced by viewing it through the prisms. As visual structure was added, the drop in heading error was significantly less with the prisms than with the computed offset. This suggests that Rushton, et al.'s (1998) null effect of optic flow may have been due to a combination of prisms and minimal flow.

This interpretation is supported by other open-field prism experiments, in which the influence of optic flow increases with visual structure. For example, Wood et al. (2000) found that walking paths became much straighter when

random markings were placed on the grass, and almost completely straight when an array of small squares were arranged in a grid pattern. Similarly, Harris and Carré (2001) reported that paths are significantly straighter when subjects crawl rather than walk, which increases the flow rate and the visual coarseness of floor texture by lowering the eye height.

Equation 5 predicts an influence of flow rate as well as visual structure on the contribution of optic flow, consistent with Harris and Carré's (2001) finding. We directly tested flow rate in the VENLab by manipulating the gain of the visual display (Fink & Warren, 2002). Participants walked at a normal speed to a target in a coarsely textured environment, while the visual gain was varied between 0.5, 1.0, 2.0, or 4.0. With a gain of 1.0, the flow speed in the display matched the participant's walking speed, whereas with a gain of 4.0, it was four times the walking speed. As before, the optic flow was randomly offset by 10° to the left or right of the walking direction. We observed a direct relation between flow rate and path straightness: as gain increased, the walking paths became significantly straighter and the virtual heading error significantly smaller. At the highest flow rate (gain=4.0), the lateral deviation of the path decreased by 33% and the heading error was reduced to 2°. This confirms an increasing contribution of optic flow with speed, as well as a residual influence of egocentric direction, as predicted by the additive model.

Following Rogers and Dalton (1999), we also examined adaptation to the visual offset to determine whether it was influenced by the available optic flow. Participants received 38 adaptation trials either in the fully textured world (floor, ceiling, wall, posts) or with a single target line (little flow). The optic flow was offset by 10°, this time always to the right, inducing walking paths that curved leftward. They were then transferred to the same or opposite environment for 10 trials, with no flow offset. An aftereffect of adaptation would thus be a path that curved rightward. Two important results stand out in the data. First, the textured world produced greater adaptation than did the target line, as revealed by a larger aftereffect when participants were transferred to the line environment. Second, when they were transferred to the textured environment, the aftereffect was abolished within one or two trials. These results indicate that participants depend upon the optic flow as a reliable "teaching signal", so that they rapidly adapt to a mismatch between optic flow and egocentric direction. This again confirms the dominance of optic flow in the visual guidance of walking to a stationary goal.

In contrast, somewhat to our surprise, we recently found no contribution of optic flow to intercepting a moving target (Fajen & Warren, 2002). In the VENLab, participants walked to a target that moved on a linear path at 0.6 m/s, but randomly varied in its initial position and direction of motion. They successfully intercepted the target by turning onto a straight path that led the target by a β angle that approached 15°-20°. However, the paths were unaffected by manipulations of the global flow from the background, which specifies the heading in the environment, or the local flow from the target itself, which specifies the heading relative to the target. This strongly suggests that steering toward a moving target is based on the egocentric direction of the target alone.

Why might this be the case? With a stationary target, the observer can bring β to zero by placing the global FOE on the target, or by nulling the motion parallax between the target and the surrounding environment. But if the target is moving the FOE is eliminated as the observer turns to track the target, and the motion parallax with the target cannot be nulled. Thus, optic flow may dominate with a stationary target when it is particularly effective for bringing β to zero, but not with a moving target to guide turning to a constant β ahead of the target. In this case egocentric direction dominates instead.

There is some disagreement as to whether the results for a stationary goal should be attributed to optic flow per se, or might be due to "alignment cues" such as local motion parallax. For example, keeping the target aligned with a nearer or farther feature on the ground by nulling the motion parallax between them would result in a straight path. Such motion parallax is in fact a local property of the optic flow, and zeroing parallax with the target is just one species of an optic flow strategy, so there is no inconsistency here. Harris and Carré (2001) reported little influence of local parallax during walking, when they manipulated the distance between the target and a background wall; however, parallax with the ground plane was still available. Similarly, when Li and Warren (2000) removed local target parallax, there was no effect on heading judgments during simulated rotation, implying that the global optic flow was sufficient to perceive heading. On the other hand, a ground texture such as a grid or checkerboard that defines a line (or lane) to the target presents a special case. One could follow a straight path to the target simply by maintaining one's position with respect to the line, without relying on optic flow at all. However, to the extent that optical rotation of the line is used to guide walking (Beal & Loomis, 1996), this case is also related to motion parallax.

Although the existing evidence is consistent with a heading strategy, there is as yet no direct evidence that the perception of heading per se is involved in the control of locomotion. The next item on the agenda for this line of research is thus to identify the specific properties of optic flow that are used to guide walking, and tease apart the particular hypotheses for steering to a goal.

4 BEHAVIORAL DYNAMICS OF LOCOMOTION

If our aim is to formulate laws of control that characterize how information modulates action, we need to have a good description of the behavioral outcome. By *behavioral dynamics*, we simply mean a description of the time-evolution of observed behavior. This way of formulating the problem allows us to formalize behavior in terms of systems of differential equations and to use methods from nonlinear dynamics to analyze perception and action. Our approach is inspired by that of Schöner et al. (1995), who developed a dynamical control system for mobile robots. In the present case, we wish to develop an empirical dynamical model of human locomotor behavior.

The behavioral dynamics of locomotion must cover the tasks of steering to a stationary goal, avoiding stationary obstacles, intercepting moving targets, and avoiding moving obstacles. Our current research program seeks to experimentally measure human walking behavior for each of these tasks, and use the data to specify a dynamical model of heading control. Once these components are modeled individually, we attempt to combine them to predict the routes that people adopt in more complex environments. A common approach to this problem is to explicitly plan a route based on a detailed world model, an internal representation of the positions and motions of all objects in the scene. But in the present approach, steering is based on current information about one's heading with respect to nearby objects, so the path emerges on-line from the interaction between agent and environment. If we can formalize the locomotor "rules" for an individual agent, this may ultimately allow us to model interactions among multiple agents in a complex environment.

4.1 Behavioral Dynamics of Steering to a Goal

Let us assume that goal-directed behavior can be described by a small number of *behavioral variables* which express aspects of action that are relevant to the goal. These define the dimensions of a *state space* for the system, and an instance of behavior can be represented as a *trajectory* in state space. Goals correspond to regions in state space to which trajectories converge, known as *attractors*, whereas states to be avoided correspond to regions from which trajectories diverge, known as *repellors*. Sudden changes in the number or type of such fixed points are known as *bifurcations*, which correspond to qualitative transitions in behavior. These trajectories may be formally expressed as solutions to a system of differential equations, and thus the problem is to formalize such a *dynamical system* whose solutions capture the observed behavior in question.

For a terrestrial agent, we take the current heading direction ϕ and turning rate $\dot{\phi}$ in the horizontal plane as behavioral variables, assuming travel at a constant speed v. From the agent's current (x, z) position, a goal lies in the

direction ψ_g at a distance d_g , and an obstacle lies in the direction ψ_o at a distance d_o . The simplest description of steering toward a stationary goal is for the agent to bring the heading error or *goal angle* between the current heading direction and the goal direction to zero, such that the heading is stabilized on the goal $\beta = \phi - \psi_g = 0$. In this basic case, the goal direction would behave like an attractor in state space at $(\phi, \dot{\phi}) = (\psi_g, 0)$. On the other hand, the simplest description of obstacle avoidance is to increase the *obstacle angle* between the current heading and the obstacle direction, $\phi - \psi_o > 0$. The obstacle direction would thus act like a repellor, or unstable fixed point, at $(\phi, \dot{\phi}) = (\psi_o, 0)$. In addition, one might suspect that object distance (or equivalently, time-to-contact) also influences behavior, for nearby obstacles should be avoided before more distant obstacles.

However, the form of the turning functions is an empirical question. Given that a physical body with inertia must undergo angular acceleration to change heading direction, it is reasonable to assume that a description of steering behavior requires at least a second-order system. To get an intuition, imagine that the agent's current heading direction is attached to the goal direction by a damped spring. Angular acceleration toward the goal would thus depend on the stiffness of the spring and be resisted by the damping. In addition, the distance of the goal would modulate the spring stiffness. At the same time, imagine that the heading direction is repelled from each obstacle by another spring, whose stiffness is modulated by the distance of the obstacle. Thus, at any moment, the heading is determined by the resultant of all spring forces acting on the agent; specifically, the current attractor direction is determined by the sum of all components. As the agent moves through the environment to the next (x,z) position, the goal angle (ψ_g) and obstacle angles (ψ_o) change and the directions of attractors and repellors shift, influencing the next heading direction. Locomotion in an environment is thus a four-dimensional system, for to predict the agent's future position we need to know it's current position (x, z), heading (ϕ) , and turning rate $(\dot{\phi})$, assuming that speed is constant.

To determine the forms of these functions, we embarked on a series of studies in the VENLab to measure how a walker's heading direction is influenced by the angles and distances of goals and obstacles (Fajen & Warren, in press). Our first experiments investigated how participants steered toward a stationary goal, as we varied the initial goal angle (0° to 25°) and goal distance (2 m to 8 m). On a given trial, the participant walked toward a marker on a textured ground plane to establish an initial direction and speed, and then a blue goal post appeared.

The results demonstrate that participants turn onto a straight path to the goal (e.g. Figure 3a), but do so more rapidly when the goal is at a greater



Figure 3. Walking to a goal at a distance of 2, 4 or 8 m. a) Mean paths with an initial goal angle of 20°. b) Mean time series of heading error with initial goal angles of $\pm 10^{\circ}$ or 20°. [From Fajen & Warren, in press; used by permission.]

angle or a closer distance. The time series of heading error show that β converges to zero from all initial conditions (Figure 3b), with an angular acceleration that increases linearly with goal angle and decreases exponentially with goal distance. The goal direction thus behaves like an attractor of heading.

We modeled this behavior with an angular "mass-spring" equation, in which angular acceleration $\ddot{\phi}$ is a function of both goal angle ($\beta = \phi - \psi_g$) and goal distance (d_g),

$$\ddot{\phi} = -b\dot{\phi} - k_{a}(\phi - \psi_{a})(e^{-c_{1}d_{g}} + c_{2})$$
(6)

The "damping" term indicates that the resistance to turning is proportional to turning rate; the *b* parameter determines the slope of this function, expressing the ratio of damping to the body's moment of inertia (in units of 1/s). The "stiffness" term reflects the finding that angular acceleration increases linearly with goal angle, at least over the tested range of -25° to $+25^{\circ}$. The k_g parameter determines the slope of this function and hence the attractiveness of the goal, expressing the ratio of stiffness to the moment of inertia (in units of $1/s^2$). Finally, the attractiveness of the goal decreases exponentially with distance to some minimum value (to ensure that the agent steers toward distant goals), so the "stiffness" is modulated by an exponential function in which c_1 determines the rate of decay and c_2 the minimum angular acceleration. Least-squares fits to the mean time series of β yielded parameter values of b = 3.25, $k_g = 7.50$, $c_1 = 0.40$, and $c_2 = 0.40$.



Figure 4. Model simulations of walking to a goal at 2, 4, and 8 m. a) Paths with an initial goal angle of 20° . b) Time series of heading error with initial goal angles of $\pm 10^{\circ}$ or 20° . [From Fajen & Warren, in press; used by permission.]

Simulations of our experimental conditions generate locomotor paths that are very close to the human data (Figure 4a), and β time series that converge to zero in a similar manner (Figure 4b). The fits to the mean time series averaged r^2 =0.98 over all conditions, indicating that model behavior is virtually identical to the mean human behavior. Thus, the model successfully captures the behavioral dynamics of walking to a goal, in which the goal direction behaves like an attractor of heading, whose strength increases with angle and decreases with distance.

4.2 Behavioral Dynamics of Obstacle Avoidance

Now consider how people avoid a stationary obstacle. In these experiments, we recorded detours taken around an obstacle en route to a goal, which presumably depend on the obstacle's position. On each trial, the participant began walking toward a green goal post, and after 1 m a blue obstacle post appeared slightly to the left or right of their path. We manipulated the initial angle between the obstacle and the path (1° to 8°) and the initial obstacle distance (3 m to 5 m), and observed their effects on the participant's heading direction. Once again, both the angle and distance of the obstacle angle β_o show that the heading was repelled from the obstacle direction, such that the curves diverge from zero in all conditions (Figure 5b). In this case, the angular acceleration decreased exponentially with both obstacle angle and obstacle distance.



Figure 5. Obstacle avoidance with an initial distance of 3, 4, or 5 m and obstacle angle of -4° . a) Mean paths. b) Mean time series of heading error (obstacle angle). [From Fajen & Warren, in press; used by permission.]

To incorporate this behavior in the model, we simply added an obstacle component to the previous goal component. The net angular acceleration is thus also a function of the obstacle angle $(\beta_o = \phi - \psi_o)$ and distance (d_o) ,

$$\ddot{\phi} = -b\dot{\phi} - k_g(\phi - \psi_g)(e^{-c_1 d_g} + c_2) + k_o(\phi - \psi_o)(e^{-c_3 | b - \psi_o |})(e^{-c_4 d_o})$$
(7)

The obstacle "stiffness" term reflects the finding that angular acceleration decreases exponentially with a positive (right) or negative (left) obstacle angle; the amplitude of this function is determined by the parameter k_o , its decay rate by c_3 (in units of 1/rad), and it asymptotes to zero. The stiffness also decreases exponentially to zero with obstacle distance, where parameter c_4 is the decay rate (in units of 1/m). Keeping the previous parameter values for the goal component fixed, we fit the extended model to the mean β time series for the obstacle data, yielding obstacle parameter values of $k_o = 198.0$, $c_3 = 6.5$, and $c_4 = 0.8$.

Simulations for the initial conditions of the obstacle experiments reproduce the human paths (e.g. Figure 6a) and the β_o time series (Figure 6b), with a mean $r^2 = .975$. Thus, the extended model captures the behavioral dynamics of obstacle avoidance, such that the obstacle direction behaves like a repellor of heading, and angular acceleration decreases with both obstacle angle and distance.



Figure 6. Model simulations of obstacle avoidance, with an initial distance of 3, 4, or 5 m and obstacle angle of -4° . a) Paths. b) Time series of heading error (obstacle angle). [From Fajen & Warren, in press; used by permission.]

It is important to note that the fitted model only relies on information about the environment within a limited window, not a full world model. In particular, the influence of obstacles asymptotes to zero at a distance of around 4 m and an angle of $\pm 60^{\circ}$ about the heading direction, and the influence of the goal asymptotes at a distance of around 8 m. This implies that a limited sample of the environment is sufficient to account for human locomotor behavior. Moreover, because the distance functions are gradually decreasing exponentials, the model can tolerate a fair amount of error in perceived distance (or time-to-contact), particularly at larger distances, without greatly affecting the steering behavior. Adding 10% Gaussian noise into the perceived distance variables only induces a standard deviation of a few centimeters in the lateral position of the path around an obstacle.

4.3 Routes as Emergent Behavior

In the steering dynamics model, a route emerges from the agent's interaction with a structured environment, rather than being explicitly planned in advance. Now that we have formulated basic components for a goal and an obstacle, the question arises as to whether the model can be used predict more complex behavior. The simplest case involves selecting one of two possible routes around an obstacle en route to a goal – the most direct route on an "inside" path, or the long way around on an "outside" path. Such a choice appears as a bifurcation in the model dynamics, and the branch that is taken depends on the agent's initial conditions.

The aim of our third study was to record the routes that people adopt around an obstacle under different initial conditions and to test whether the parameterized model can account for them (Fajen & Warren, in press). On each trial, the participant walked toward a marker for 1 m, and then both a blue goal post and a red obstacle post appeared. The obstacle lay between the heading direction and the goal direction at a distance of 4 m, such that the participant was initially heading on an outside path. The position of the obstacle was manipulated so that the goal-obstacle angle varied from 1° to 8°, while the attractiveness of the goal was manipulated by varying its initial distance from 5 to 7 m. This allowed us to test the conditions under which participants switch from an outside to an inside route.

Participants switched to an inside path when the initial goal-obstacle angle increased to 2°-4°, and as the goal got closer. When we tested the model with the previous parameter values, it exhibited the same pattern of switching, although the switch occurred at a somewhat higher angle, indicating that the model was biased toward outside paths. This may be because our first experiments did not sample cases in which the participant had to cross in front of an obstacle. However, adjusting a single obstacle parameter, from c_4 =0.8 to 1.6, was sufficient to induce the switch in the human range. Parameter c_4 might be thought of as a "risk" parameter, for increasing it makes the repulsion decay more rapidly with distance, allowing a closer approach to obstacles. Thus, the agent's risk level and body size are implicitly represented in the model by this parameter. These parameter values were held fixed for the remaining experiments.

Such route switching behavior results from competition between the attractiveness of the goal, which increases with the angle and nearness of the goal, and the repulsion of the obstacle, which decreases with angle. If the obstacle is positioned between the agent and the goal, the model is bistable, such that both outside and inside heading directions are attractive; the one that is selected depends on the agent's initial conditions. As the agent moves around the obstacle, the model shifts to only one stable heading, exhibiting a *tangent bifurcation* (see Fajen & Warren, in press). Thus, switching behavior and route selection can be understood as a consequence of bifurcations and attractors in the underlying dynamics of the system.

Whereas the model produces a unique path for each set of initial conditions, human routes are more variable. We wanted to see whether simply adding noise to the model would be sufficient to simulate the relative frequency of inside and outside paths. We thus added error to each perceptual variable and parameter independently at the onset of a trial, drawn from a Gaussian distribution with a standard deviation of 10%. The agent's initial x position and heading direction were also randomly varied, matching the human standard deviations. The resulting simulations effectively reproduced the distribution of inside and outside paths across environmental conditions in the human data (Fajen & Warren, in press).

These results demonstrate that simple route selection can be accounted for as a consequence of the on-line steering dynamics for goals and obstacles. But what about routes through more complex environments? One advantage of the present model is that it scales linearly with the complexity of the scene, simply adding one term for each object in the immediate environment. Thus, in principle, we could predict locomotor paths by continuing to add a term for each new obstacle, while holding parameter values fixed.

We first tested this prediction with a configuration of two obstacles en route to a goal straight ahead (Fajen & Warren, 2001). The nearer obstacle was in a fixed position slightly to one side of the goal direction, whereas the farther obstacle was manipulated so its initial goal-obstacle angle varied from 0° to 10°. As this angle increases, the model predicts a particular sequence of route switching: from the outside of the far obstacle, to the outside of the near obstacle, and finally to a route between them. Participants demonstrated exactly this sequence of switching. Once again there was some variability in human route selection, but the distribution of paths was closely reproduced by adding 10% Gaussian noise to the model's perceptual variables and parameters at the onset of a simulated trial (Fajen et al., 2002).

A strong test is whether the model can predict human routes through a complex field of obstacles, simply by adding terms with fixed parameters to the equation. To examine this possibility, we recorded participants walking through random arrays of 12 yellow posts to get to a blue goal post (Warren et al., 2001). The model did a reasonable job of reproducing the human paths (e.g. Figure 7). One measure of model performance is the number of obstacles by which the model differed from the most frequent human path. On half of the eight arrays they were identical, on two arrays they differed by only one obstacle, and on the remaining two arrays they differed by two and four obstacles. Of course, there was once again some variability in human paths across trials and individuals (see Figure 7). Given the number of bifurcation points in such an environment, behavior in this case is particularly susceptible to influences at multiple time scales that could affect the current state of the participant and send them down a different path. These might include variations in the initial walking direction, the foot one is currently on, the obstacles to which one is attending, and the adaptive history of one's postural state. We are currently trying to simulate the distribution of human paths by adding noise to perceptual variables and parameters at each step en route. But the deeper point is that the model captures the qualitative structure of



Figure 7. Routes to a goal (X) through an array of 12 obstacles (O), for two participants (S2 and S5). Dotted curves represent 6 trials from each participant, solid curves represent the model simulation. Starting point is at (0,0).

locomotor paths and route switching in terms of the dynamics of attractors, repellors, and bifurcations.

One limitation of the model is that all obstacles are currently treated as points. This may be adequate for posts, but is unrealistic for environments that contain large obstacles or extended surfaces such as walls. One solution may be to adjust the decay rate of the repulsion function for each obstacle (parameter c_3) based on its visual angle, or to treat a fat obstacle as a set of points at finite intervals and sum their influence.

In sum, human route selection can be understood as a form of emergent behavior, resulting from an agent with certain steering dynamics interacting with a structured environment. Somewhat surprisingly, the influences of objects in the environment can be treated as independent and additive, so the model scales linearly with the complexity of the scene. Yet nonlinear behavior such as route switching emerges from the interactions of attractors and repellors. The results demonstrate that the on-line steering dynamics are empirically sufficient to account for human locomotor paths, even in fairly complex environments, rendering explicit path planning and an internal world model unnecessary.

4.4 Behavioral Dynamics of Intercepting a Moving Target

Thus far we have modeled locomotion with increasingly complex configurations of stationary goals and obstacles. But people typically operate in a dynamic environment in which some goals and obstacles are moving – for example, walking through a busy train terminal to catch a friend. We have begun to model such dynamic situations by investigating the case a moving target (Fajen & Warren, 2002).



Figure 8. Walking to a moving target. a) Pursuit strategy. b) Interception strategy.

If people walk to a moving target the same way they do to a stationary one, they would simply head in the current direction of the target. Such a *pursuit strategy* would result in a curved path of locomotion (Figure 8a), as the walker continually changes direction to track the target. Alternatively, the walker might try to intercept a moving target by walking ahead of it, which we call an *interception strategy* (Figure 8b). A good example is the open-field tackle in American football, in which the defenseman tries to cut off the ballcarrier by running on a short, straight interception path.

The interception path may be determined as follows. The ball-carrier's velocity (u) has two components, a radial component toward the defenseman (u_r) , and a transverse component in the perpendicular direction (u_t) . A defenseman moving with velocity (v) must first match the ball-carrier's transverse component ($v_t = u_t$), reducing it to a one-dimensional problem. Then he or she must approach the ball-carrier $(v_r > u_r)$. If both players are traveling at constant velocities, this yields a straight path to the interception point with a constant angle β between the heading direction and the target direction. But even if the ball-carrier's velocity changes, maintaining these conditions in a closed-loop manner will lead to successful interception. One way to implement the interception strategy is to perceive the distal velocity of the target and compute the required β ($\hat{\beta} = \sin^{-1}(u_{\ell}/v)$). Alternatively, one could try to adopt a straight path that keeps β constant, effectively nulling $\dot{\beta}$. Sailors are familiar with this constant bearing strategy, for if another boat approaches with a constant β , it is a clear indicator that you are on a collision course.

To investigate this question, we asked participants to walk to moving targets in a textured environment the VENLab. The target was a blue post that moved with a constant velocity. On each trial, the participant walked forward for 1 m, whereupon the target appeared at a distance of 3 m; its initial angle



Figure 9. Intercepting a moving target on foot. a) Mean path for target initially straight ahead (top) or 25° to the left (bottom). The target (O) moves laterally. b) Mean time series of obstacle angle β for the same initial conditions.

from the heading and its direction of motion were varied across trials. It turns out that participants do not simply adopt straight paths with constant interception angles, but rather exhibit transient dynamics (Figure 9): they gradually turn onto a straight path and decelerate as they arrive at the target, while β approaches the expected angle and then falls to zero.

We modeled this interception behavior with a simple modification of the goal component. In order to null $\dot{\beta}$, we substituted it for β in the stiffness term:

$$\ddot{\phi} = -b\dot{\phi} - k_{g}(\dot{\phi} - \psi_{g})(e^{-c_{1}d_{g}} + c_{2})$$
(8)

Consequently, angular acceleration goes to zero as both the turning rate ($\dot{\phi}$) and the change in target-heading angle ($\dot{\beta} = \dot{\phi} - \psi_t$) go to zero. The "stiffness" term thus yields a constant β , while the "damping" term tends to produce a straight path, thereby avoiding the infinitely many equi-angular spiral paths that also hold β constant. We modeled the detection of target motion at the onset of a trial with a sigmoidal function having a latency of 0.5 s. Based on the human data, we held walking speed constant (1.42 m/s) with a final deceleration in the last half-second before contact with the target. Fitting this model to the mean time series of β resulting in parameter values of b = 7.00, $k_r = 0.17$, $c_1 = 0.013$, and $c_2 = 0.45$.

Model simulations yielded interception paths that were very similar to the walking data (Figure 10). The time series of β also closely matched the evolution of mean target-heading angle, with $r^2 = 0.92$. We also determined that the final drop in β is due to the deceleration near contact, which might be



Figure 10. Model simulations of intercepting a moving target, for the same initial conditions as Figure 9. a) Locomotor path. b) Time series of obstacle angle β .

controlled by the optical expansion of the target (Lee, 1976; Yilmaz & Warren, 1995).

Thus, the null- $\dot{\beta}$ strategy is sufficient for controlling interception with a moving target. It is interesting to note that simulations in which the required constant β is explicitly computed from distal target velocity produced nearly identical behavior, even when the parameters were the same as those for a stationary goal. This version has the advantage of reducing to the stationary goal model when target speed is zero, yielding a smooth transition between stationary and moving targets – but at the price of explicit computation from additional informational variables. This observation raises an important question about the organization of behavior: is there a switch between two distinct strategies for stationary and moving targets, or a single continuous strategy? In either case, a perceptual threshold for the detection of target motion could yield what appears to be nonlinear switching behavior.

The next step in this research program is to study the avoidance of moving obstacles, such as other pedestrians. Most simply, the model might be extended to a moving obstacle by flipping the sign of the "stiffness" term, turning the interception point from an attractor into a repellor of heading. Successfully modeling these four basic locomotor components would then permit us to investigate their interactions, such as walking to a moving target while avoiding stationary or moving obstacles. Once the locomotor "rules" for an individual agent are worked out, this may allow us to simulate interactions among multiple agents and structured environments, such as pedestrian traffic flow and crowd behavior.

5 CONTROL LAWS FOR LOCOMOTION

Let us return briefly to our original question, how perceptual information is used to control locomotor behavior. Now that we have a formal description of the behavioral dynamics of locomotion, we can see how information plays a role by contributing to the dynamics, rather than directly determining behavior. In particular, it is possible to consider whether specific control laws can give rise to the observed behavior.

Schöner, et al. (1995) developed a control system for a mobile robot based on a first-order dynamical system, which is always in an attractor state and thus always stable. The advantage of such a system is that it can assure a stable solution under multiple constraints, such as goals and obstacles in arbitrary positions. In contrast, observed behavior is a consequence of such control laws interacting with the physics of the agent and its environment. For example, an inertial body must angularly accelerate and decelerate, such that the actual heading lags behind the intended heading. Our model of the behavioral dynamics is thus a higher-order system that treats steering adjustments as transient behavior toward the current attractor. The question is whether a first-order control law could give rise to such higher-order behavior.

To test this idea, our colleague Philip Fink simulated a first-order control law that is embedded within a second-order system representing the physical agent. Given that our model captures the influence of goals and obstacles, we used the same form for the control law,

$$\dot{\phi}' = -k_g (\phi - \psi_g) (e^{-c_1 d_g} + c_2) + k_o (\phi - \psi_o) (e^{-c_3 |\phi - \psi_o|}) (e^{-c_4 d_o})$$
(9)

The control law is thus a first-order system that immediately relaxes to an attractor for the intended heading in the direction ϕ^* , which is determined by the current configuration of goals and obstacles. The angular acceleration of the body toward this intended heading is then determined by a second-order system with fixed parameters,

$$\ddot{\phi} = -b_b \dot{\phi} - k_b \left(\phi - \phi^* \right) \tag{10}$$

Due to the body's inertia, the actual heading lags behind the intended heading, so the observed behavior is transient. When this model was tested with one obstacle en route to a goal (Section 4.2), the paths were nearly identical to those of our original model and the time series of β fit the mean human data with an $r^2 = 0.991$ (for parameter values $k_g = 59.1625$, $c_1 = .0555$, $c_2 = .01125$, $k_o = 842$, $c_3 = 2.74063$, $c_4 = .04653$, $b_b = .0375$, $k_b = 592$). Thus, the behavioral

dynamics can be accounted for by a 1st-order control law driving a 2nd-order body.

Finally, the control law incorporates certain perceptual variables, including the angle between the current heading direction (ϕ) and an object's current direction (ψ), as well as the object's current distance (d). As reviewed in Section 2, the direction of heading is redundantly specified by optic flow and the proprioceptive locomotor axis, whereas the direction of a goal or obstacle is given by its visual direction. We previously determined that both optic flow and proprioception contribute to walking to a goal (Eq. 5), (Warren et al., 2001). Thus, we may expand the informational term in the goal component of Eq. 9 as

$$\phi - \psi_g = \left(\phi_{loco} - \psi_g\right) + wv \left(\phi_{flow} - \psi_g\right) \tag{11}$$

We have yet to empirically test whether the same relation holds for the obstacle component. Note that the distance of an object may be specified either by static distance information such as its angle of elevation on the ground plane or stereoscopic depth. Alternatively, equivalent information over short distances may be provided by the first-order time-to-contact with the object.

Such dynamical control laws are quite different from a simple mapping between an optical variable and a movement variable. Rather than directly determining the kinematics of the movement, the control law determines an attractor for the intended action, thereby modulating the dynamics of the system. This is converted into a force and thence an angular acceleration, resulting in the observed behavior.

6 CONCLUSION

In this chapter we have sought to present an integrated account of perceptually guided locomotion. On our view, such an account must include the multi-sensory information for self-motion, the control laws by which that information modulates the action system, and the behavioral dynamics to which they give rise. Locomotor paths and choices about routes can then be understood as emergent behavior, which unfolds as an agent interacts with a structured environment. Locomotion offers a relatively simple case study in how adaptive behavior can emerge from information and dynamics. It is our belief that it provides a model for the way in which such processes of pattern formation give rise to more complex forms of human behavior.

303

ACKNOWLEDGMENTS

This research was supported by grants from the National Institutes of Health (EY10923, KO2 MH01353) and the National Science Foundation (LIS IRI-9720327). Permission to reproduce Figures 1, 3-6, and 8 was obtained from the American Psychological Association, and Figure 2 from the Nature Publishing Group.

REFERENCES

- Banks, M. S., Ehrlich, S. M., Backus, B. T., & Crowell, J. A. (1996). Estimating heading during real and simulated eye movements. *Vision Res.*, *36*, 431-443.
- Beal, A. C., & Loomis, J. M. (1996). Visual control of steering without course information. *Perception*, 25, 481-494.
- Crowell, J. A., & Andersen, R. A. (2001). Pursuit compensation during self-motion. *Perception*, 30, 1465-1488.
- Cutting, J. E., Springer, K., Braren, P. A., & Johnson, S. H. (1992). Wayfinding on foot from information in retinal, not optical, flow. J. Exp. Psychol. Gen., 121, 41-72.
- Duchon, A. P., & Warren, W. H. (2002). A visual equalization strategy for locomotor control: Of honeybees, robots, and humans. *Psychol. Sci.*, 13, 272-278.
- Duffy, C. J. (in press). The Cortical Analysis of Optic Flow. In: L. M. Chalupa & J. S. Werner (Eds.), *The Visual Neurosciences*. Cambridge, MA: MIT Press.
- Fajen, B. R., & Warren, W. H. (2002). Behavioral dynamics of intercepting a moving target on foot, *(submitted)*.
- Fajen, B. R., & Warren, W. H. (in press). Behavioral dynamics of steering, obstacle avoidance, and route selection. J. Exp. Psychol. Hum. Percept. Perform.
- Fink, P. W., & Warren, W. H. (2002). Velocity dependence of optic flow strategy for steering and obstacle avoidance. Paper presented at the Vision Science Society, Sarasota, FL.
- Frey, B. F., & Owen, D. H. (1999). The utility of motion parallax information for the perception and control of heading. J. Exp. Psychol. Hum. Percept. Perform., 25, 445-460.
- Gibson, J. J. (1958/1998). Visually controlled locomotion and visual orientation in animals. *Br. J. Psychol.*, 49, 182-194., Reprinted in *Ecol. Psychol.*, 10, 161-176.

- Gibson, J. J. (1966). The Senses Considered as Perceptual Systems. Boston, MA: Houghton-Mifflin.
- Gibson, J. J. (1979). The Ecological Approach to Visual Perception. Boston: Houghton Mifflin.
- Harris, M. G., & Carre, G. (2001). Is optic flow used to guide walking while wearing a displacing prism? *Perception*, 30, 811-818.
- Land, M. (1998). The Visual Control of Steering. In: L. R. Harris & H. Jenkins (Eds.), *Vision and Action*. Cambridge University Press.
- Land, M. E., & Lee, D. N. (1994). Where we look when we steer. Nature, 369, 742-744.
- Lappe, M., Bremmer, F., & van den Berg, A. V. (1999). Perception of self-motion from visual flow. *Trends Cogn. Sci.*, 3, 329-336.
- Lee, D. N. (1976). A theory of visual control of braking based on information about time-tocollision. *Perception*, 5, 437-459.
- Lee, D. N. (1980). Visuo-motor Coordination in Space-Time. In G. E. Stelmach & J. Requin (Eds.), *Tutorials in Motor Behavior* (pp. 281-295). Amsterdam: North-Holland.
- Lee, D. N. (1998). Guiding movement by coupling taus. Ecol. Psychol., 10, 221-250.
- Lee, D. N., van der Weel, F. R., Hitchcock, T., Matejowsky, E., & Pettigrew, J. D. (1992). Common principles of guidance by echolocation and vision. J. Comp. Physiol. A, 171, 563-571.
- Lee, D. N., & Young, D. S. (1985). Visual Timing of Interceptive Action. In D. Ingle & M. Jeannerod & D. N. Lee (Eds.), *Brain Mechanisms and Spatial Vision* (pp. 1-30). Dordrecht, The Netherlands: Martinus Nijhoff.
- Li, L., & Warren, W. H. (2000). Perception of heading during rotation: sufficiency of dense motion parallax and reference objects. *Vision Res.* 40, 3873-3894.
- Li, L., & Warren, W. H. (2002). Retinal flow is sufficient for steering during simulated rotation. *Psychol. Sci.*, 13, 485-491.
- Nakayama, K. (1994). James Gibson -- An appreciation. Psychol. Rev., 101, 329-335.
- Perrone, J. A. (1992). Model for the computation of self-motion in biological systems. J. Opt. Soc. Am. A, 9, 177-194.
- Rieger, J. H., & Lawton, D. T. (1985). Processing differential image motion. J. Opt. Soc. Am. A, 2, 354-360.
- Rogers, B. J., & Allison, R. S. (1999). When do we use optic flow and when do we use perceived direction to control locomotion? *Perception, 28 (Suppl), 2.*

- Royden, C. S., Banks, M. S., & Crowell, J. A. (1992). The perception of heading during eye movements. *Nature*, 360, 583-585.
- Royden, C. S., Crowell, J. A., & Banks, M. S. (1994). Estimating heading during eye movements. *Vision Res.*, 34, 3197-3214.
- Royden, C. S., & Hildreth, E. C. (1996). Human heading judgments in the presence of moving objects. *Percept. Psychophys.*, 58, 836-856.
- Rushton, S. K., Harris, J. M., Lloyd, M., & Wann, J. P. (1998). Guidance of locomotion on foot uses perceived target location rather than optic flow. *Curr. Biol.*, 8, 1191-1194.
- Rushton, S. K., Harris, J. M., & Wann, J. P. (1999). Steering, optic flow, and the respective importance of depth and retinal motion distribution. *Perception*, *28*, 255-266.
- Saunders, J. A., & Warren, W. H. (1996). Perceived heading biased by a moving object: effects of disparity and object position. *Invest. Ophthalmol. Vis. Sci.*, 37, S454.
- Schöner, G., Dose, M., & Engels, C. (1995). Dynamics of behavior: Theory and applications for autonomous robot architectures. *Rob. Auton. Sys.*, 16, 213-245.
- Srinivasan, M. V. (1998). Insects as Gibsonian animals. Ecol. Psychol., 10.
- Stone, L. S., & Perrone, J. A. (1997). Human heading estimation during visually simulated curvilinear motion. Vision Research, 37, 573-590.
- Telford, L., Howard, I. P., & Ohmi, M. (1995). Heading judgments during active and passive self-motion. *Exp. Brain Res.*, 104, 502-510.
- van den Berg, A. V. (1992). Robustness of perception of heading from optic flow. *Vision Res.*, 32, 1285-1296.
- van den Berg, A. V. (1996). Judgements of heading. Vision Res., 36, 2337-2350.
- Wang, Y., & Frost, B. J. (1992). Time to collision is signalled by neurons in the nucleum rotundus of pigeons. *Nature*, *356*, 236-238.
- Warren, W. H. (1988). Action Modes and Laws of Control for the Visual Guidance of Action. In O. Meijer & K. Roth (Eds.), *Movement Behavior: The Motor-Action Controversy* (pp. 339-380). Amsterdam: North Holland.
- Warren, W. H. (1998). Visually controlled locomotion: 40 years later. *Ecol. Psychol.*, 10, 177-219.
- Warren, W. H. (2002). The dynamics of perception and action. (Unpublished manuscript).
- Warren, W. H. (in press). Optic Flow. In: L. M. Chalupa & J. S. Werner (Eds.), *The Visual Neurosciences*. Cambridge, MA: MIT Press.

- Warren, W. H., & Hannon, D. J. (1988). Direction of self-motion is perceived from optical flow. Nature, 336(6195), 162-163.
- Warren, W. H., & Hannon, D. J. (1990). Eye movements and optical flow. J. Opt. Soc. Am. A, 7(1), 160-169.
- Warren, W. H., & Kay, B. A. (1997). Control law switching during visually guided walking. *Abs. Psychonomic Soc.*, 2, 52.
- Warren, W. H., Kay, B. A., Zosh, W. D., Duchon, A. P., & Sahuc, S. (2001). Optic flow is used to control human walking. *Nat. Neurosci.*, 4, 213-216.
- Warren, W. H., & Saunders, J. A. (1995). Perception of heading in the presence of moving objects. *Perception*, 24, 315-331.
- Warren, W. H., & Yaffe, D. M. (1989). Dynamics of step length adjustment during running. J. Exp. Psychol. Hum. Percept. Perform., 15, 618-623.
- Warren, W. H., Young, D. S., & Lee, D. N. (1986). Visual control of step length during running over irregular terrain. J. Exp. Psychol. Hum. Percept. Perform., 12, 259-266.
- Wood, R. M., Harvey, M. A., Young, C. E., Beedie, A., & Wilson, T. (2000). Weighting to go with the flow? *Curr. Biol.*, 10, R545-R546.
- Yilmaz, E. H., & Warren, W. H. (1995). Visual control of braking: a test of the tau-dot hypothesis. J. Exp. Psychol. Hum. Percept. Perform., 21, 996-1014.