WHAT NEUROLOGICAL PATIENTS TELL US ABOUT THE USE OF OPTIC FLOW?

Lucia M. Vaina [1,2] and Simon K. Rushton [3,4]

1. Boston University, Brain and Vision Research Laboratory, Department of Biomedical Engineering and Neurology, 44 Cummington St., Boston, Ma 02215, U.S.A.

2. Department of Neurology, Harvard Medical School, Brigham and Women Hospital & Massachusetts General Hospital, 75 Francis St., Boston, Ma 02215, U.S.A.

3 Cambridge Basic Research, Nissan Research & Development, Inc. Four Cambridge Center, Cambridge, MA 02142, U.S.A.

4 Department of Clinical Psychology, Astley Ainslie Hospital, Grange Loan, Edinburgh. Scotland, EH9 2HL, U.K.

Correspondence to:

Professor Lucia M. Vaina Ph.D. D.Sc.
Brain and Vision Research Laboratory
Biomedical Engineering
44 Cummington St.
Boston University
Boston, Ma 02215

Tel: +1 617 353 2455
Fax: +1 617 353 6766
Email: vaina@bu.edu

Abstract

Neurophysiological and behavioral studies, in monkeys and humans, have been used to investigate the neuronal and computational substrate of optic flow processing. Do the documented neuronal and psychophysical sensitivities to flow result from the use of flow in the guidance of locomotion? Flow research has reached maturity and now is necessary to rigorously assess whether implicit assumptions about the role of flow hold true. We suggest that the study of neurological patients may provide researchers with a critical test of the flow theory for locomotion. In this chapter we report data from several neurological patients, their psychophysical performance on optic flow tasks and observed co-occurring locomotor competencies.

Introduction

As we move through the environment the pattern of visual motion on the retina provides rich information about our passage through the scene. It is widely accepted that this information, termed “optic flow” is used to encode self-motion, orientation, visual navigation in the three-dimensional space, perception of object movement, collision avoidance, visual stabilization, and the control of posture and locomotion. The nature and properties of the mechanisms involved in the perception of optic flow have been extensively studied with physiological, psychophysical and computational methods and are the focus of other chapters in this volume (**Andersen, Bremmer, van DerBerg, Duffy, Lappe**). In this chapter we describe research with neurological patients and what such research may tell us about perception and control of locomotion.

Functional architecture of motion for navigation

The posterior parietal cortex (PPC), a region encompassing several visually responsive areas (for a review, (Andersen 1990, Andersen 1997, Andersen, et al. 1996, Andersen, et al. 1997)), is the primary neural substrate for the visual processing which could support guidance of movement using optic flow. Electrophysiological studies have demonstrated that the dorsal portion of the middle superior temporal area (MSTd) in the macaque PPC contains neurons highly responsive to specific kinds of optic flow patterns and to stereomotion (motion in depth). Microstimulation of MSTd neurons biases heading judgements (Britten and van Wezel 1998) strengthening the view that this area is involved in mediating the perception of direction of heading. However, MSTd is not the only region of brain activity directly involved in heading and other tasks of visual navigation. Other areas in the parietal lobe (Maunsell and Essen 1983a, Maunsell and Essen 1983b, Ungerleider and Desimone 1986) of the macaque brain such as the ventral intraparietal cortex (VIP), the superior temporal polysensory area

(STP), and area 7a are highly sensitive to optic flow stimuli, and to speed and direction of motion (Duhamel, et al. 1997, Read and Siegel 1997, Schaafsma, et al. 1997, Siegel and Read 1997). It is possible that different forms of optic flow may activate neurons in different areas.

There is ample evidence for several motion streams, in addition to the classic V1-MT-MST, and thus it remains important to quantitatively explore response in these other areas to flow stimuli. For example, physiological studies report that both V2 and V3 contain a high percentage of direction selective cells, and they both have significant projections to directionally selective areas including MT, VIP and the floor of the superior temporal sulcus (FST). Area V3 also contains neurons that respond to more global patterns of motion, (Gegenfurtner, et al. 1997) and FST neurons respond to complex object motion. Together with the classic V1-MT-MST visual motion processing stream, these results suggest a more loose hierarchy in the motion system of the macaque and a higher degree of parallelism than previously assumed. They also suggest a distribution of computational responsibilities among different areas.

Most studies to date have employed an abstraction of the flow field, a sparse field of small, fixed size, luminance defined moving dots. The natural flow field, however, is characterized by a broader spatial, temporal and chromatic profile, persisting, trackable objects with sharp edges and identifiable surfaces. The responses of visually responsive areas to the richer natural flow field remains to be characterized. Until that time the data collated must be viewed as partial.

In humans, functional neuroimaging studies (PET and fMRI) have repeatedly reported that many regions in the human brain respond selectively to moving patterns (Dupont, et al. 1994, Tootell, et al. 1996, Tootell, et al. 1995b). Most studies have concentrated on the region in the ascending limb of the inferior temporal sulcus referred to as hMT+ because it

functionally represents the human homologue of the macaque areas MT and MST (Beauchamp and DeYoe 1996, Cheng, et al. 1995, Dale, et al. 1995, Dale, et al. in revision, Tootell, et al. 1995a, Tootell, et al. 1994, Tootell, et al. 1993a, Tootell, et al. 1993b, Tootell, et al. 1995c). The posterior part is bounded by area V3A, which is also quite sensitive to motion (Tootell, et al. 1997). An area anterior to V3A has been designated KO, to reflect sensitivity to the form of structured kinetic stimuli (Dupont, et al. 1997). A preliminary report of a PET study from Orban's group shows that hMT is activated in heading tasks, but only marginally (Peuskens et al., 1999). The main areas of activation were seen in the human homologues of V2, V3 and V3A bilaterally, and in the posterior parietal regions. Additional motion responsive regions have been described in the occipital, occipital-parietal, occipital-temporal, and temporal and parietal regions. Taken together, these studies suggest that in humans, similar to the macaque, motion does not relate specifically to the classical distinction of the "dorsal" and "ventral" streams.

But the functional neuroimaging studies have told us little about the computations for which the visual areas in humans are responsible. Moreover, on their own they seldom can relate to models of visual behavior. Studies of patients can help bridge this important gap.

Why study motion impaired neurological patients?

In a review of the work of Gibson and those who had followed his research program, Nakayama (Nakayama 1994) noted that the psychophysical work that had been carried out had not established more than the possibility that humans could use optic flow in natural locomotion. Since then considerably more psychophysics, computational modeling and neurophysiology has been done, but as Warren more recently (Warren 1999) notes the issue of what information and strategies are actually used has still to be properly addressed. A fundamental problem as Warren points out is that many alternative models of the control of

locomotion are functionally equivalent under normal circumstances, i.e. they all predict the same behavior. It requires inventive manipulations of visual information to create circumstances under which models predict different behavior, we expand on this point in the next section. Warren and colleagues have recently begun to tackle this problem through the use of Virtual Reality technology (Warren, personal communication).

A complementary approach is the study of neurological patients. Such studies have possibly provided the earliest and certainly the most convincing evidence that, in humans, motion is a "special visual perception" (Riddoch 1917) and Goldetein & Gelb, 1918, 1923. supported by a functional-anatomical architecture similar to that suggested by anatomical, physiological and behavioral studies in the macaque monkey. More critically is that the same neurological studies reveal the role of motion in perception and action. For example, Goldstein and Gelb's (1923) patient. Schn, was unable to experience real or apparent movement in any condition, he was able to see correctly changes in position of objects and therefore could infer that they were moving. He also failed to perceive movement in depth. Patient Sch is very similar to the most extensively studied "motion blind" patient, L.M. (Shipp, et al. 1994, Zihl, et al. 1989, Zihl, et al. 1991, Zihl, et al. 1983). L.M. lives a very uncomfortable visual perceptual life because she fails to see movement of movement of objects. For her, the movement of a car looks like a series of discrete "stills" advancing in time, and therefore she finds it disconcerting to cross the street in on-coming traffic. A car seems to her far away at one moment, and dangerously close the next, with no smooth progression in between. She is unable to perceive continuous motion, tea poured from a kettle appears to her as a static solid curved cylinder. She feels handicapped in social settings when conversing with other people because she cannot perceive and therefore read mobile facial expressions. As pointed out by Nakayama (Nakayama 1985) this suggests that motion processing could play a major role in reading facial expressions, something not hitherto suspected. However, and amazingly, L.M. can see and recognize without

difficulty “biological motion” in the well known Johansson’s demonstration (Johansson 1973, Marcar, et al. 1997, McLeod, et al.). [1]She also can catch a ball thrown straight at her (McLeod, personal communication), although not when its trajectory is of to one side. What motion information, if at all, is she using to perform these tasks?

Cases such as the “motion blind” patient, L.M., are very rare. Normally loss of motion sensitivity is more sparing and selective, and studies of such patients provide important insights into the functional organization of the human visual motion systems.

For example, our patient, A.F. (Vaina, et al. 1990a, Vaina, et al. 1990b) with bilateral lesions in the posterior parietal lobes, was severely impaired on several, but not all, low level motion tasks, and like to L.M., promptly recognized the “biological motion” stimuli, could catch a ball thrown directly at him, and even could recognize 3D structure from-motion.

On the other hand, patient R.J. (Vaina, et al. 1999b), with a lesion in the anterior portion of the right temporal lobe, performed normally on both low level motion tasks, and was able to recover both 2D and 3Dstructure from motion, but he failed to recognize the human figure depicted in Johansson’s display. These reports tell us about dissociations within the motion system. Another example is the demonstration that first- or second-order motion can be selectively impaired in patients (Vaina and Cowey 1996, Vaina, et al. 1999a, Vaina, et al. 1996a, Vaina, et al. 1998b) and these studies provide compelling evidence for the hypothesis that first- and the second- order motion processes are mediated by different, parallel pathways and a novel model that accounts for these and other (Greenlee and Smith 1997, Plant, et al.) findings was put forward by Clifford et al, 1999 (Clifford and Vaina 1998).

Psychophysical studies of patients performance on an a priori defined set of motion tasks can provide an important benchmark for the biological validity of existing computational

[1] Johnasson placed 12 small light bulbs on the head and main joints of one or two human actors, and made a movie in which only the light sources were visible. When the actors were static, all that one could see were a set of 12 as

models. For example, the double dissociation of deficits on perception of motion discontinuity and motion coherence (Vaina, et al. 1998a, Vaina, et al. 1994b) rules out models based on Random Markov Fileds and Line Processors (Koch, et al. 1989), popular in computer vision, as the only explanation of how the human brain processes motion discontinuity.

Furthermore, the performance of patients on specific perceptual tasks can reveal the necessary anatomical substrate for that task. For example, King et al, 1996 (King, et al. 1996), in a study of the residual visual sensitivity in patients deprived of the cortical pathway following either functional or anatomical hemispherectomy, found that they had neither electrodermal responses nor any conscious experience of the direction of motion in complex motion patterns (radial or circular). They interpreted their results as suggesting that the subcortical visual pathways which survive hemispherectomy and which can certainly subserve some visual processing, are insufficient to process information about direction in complex motion.

Although the foregoing examples provide only a very incomplete list of neurological studies reporting particular dissociations of motion processes, they illustrate the importance of careful quantitative studies of neurological patients in elucidating the functional architecture of the human visual motion system. In particular, such studies often provide evidence for the existence of several motion subsystems and their computational characteristics. Even more importantly, neurological studies also tell us about the putative functional roles of these various subsystems and, as Pollen (Pollen 1999)noted they “open the way for improved models based on refutations or confirmations of the present set of proposals”.

The radial flow field.

12 static dots unrecognizible as any meaningful shape. But when the actors performed various actions, or when two actors walked together and shook hands, observers could immediately recognize the actions.

During locomotion you control your direction of heading. Psychophysical judgement tasks demonstrate that direction of heading can be recovered from the instantaneous velocity flow field (Warren, et al. 1991). Neural areas such as MST have been shown to be responsive to optic flow stimuli. Therefore, it follows that MST compute the direction of heading which is then used to guide locomotion.

Although the above is a compelling theory it is necessary to question it. Does optic flow guide locomotion? There are a number of ways mobile observers could visually guide themselves around an environment. Consider walking to a target. First, observers could recover their instantaneous direction of heading, and/or path from the velocity flow field and use this information for guiding locomotion. Second, they could use cruder velocity field based iterative strategies, such as equalizing the flow to the left and right of the target (Duchon and Warren 1998, Srinivasan, et al. 1991) or canceling any rotational flow. Third, they could use the relative displacements of other objects in the scene (Cutting 1986, Cutting 1992) to determine their heading and use that for guiding locomotion. Fourth, they could use the ego-centric direction of the target and a simple alignment strategy to reach their target (Rushton, et al. 1998) or target drift (Llewellyn 1971).

The psychophysical and neurophysiological demonstrations of sensitivity to radial flow have been taken as powerful evidence that flow guides locomotion. However, this does not necessarily follow because, as argued above, there are a range of other tasks that optic flow might be used to perform. For example, radial flow may provide important information for the control of action and posture. In an elegant demonstration, (Lee 1974, Lee 1975) showed that vision is the dominant source of information in the control of vertical posture with their "swinging room" experiments. In these experiments, an observer stands upright whilst a room is swung around them. It is found that the observer swings in synchrony with the room. This

co-ordination of change of posture with the movement of the room may be through a process that nulls expansion and contraction in the global flow field. A recent elegant neurophysiological study of (Duffy and Wurtz 1996) investigated the effects of optic flow on posture in the macaque monkeys. In particular, these authors wanted to learn whether presentation of the same optic flow patterns that elicit neuronal responses in the area MST will also alter the animal's posture. Furthermore they tested whether lesioning the areas MT and MST would alter posture. In the neurophysiological experiments they observed in some trials postural sway that was dependent of the characteristics of the optic flow pattern. However, in many trails posture was not affected by the optic flow patterns, suggesting that other factors may also influence posture (e.g. vestibular and prorpioceptive). Bilateral lesions in the MT&MST areas resulted in postural instability, and these authors suggested that the "disruption of the normal visual motion processing might have lead to degraded postural control signals".

For standing posture, early psychophysical studies (Ambland and Carblanc 1980) reported peripheral dominance, but more recent experiments (Andersen 1989) suggest that postural sway can be elicited by central stimulation, using both translational and radial flow (in the central 15deg). In a series of clever experiments Stoffregen (Stoffregen 1985, Stoffregen 1986) found that both radial and translational flow patterns induced postural sway when presented in central vision, while only translational flow was effective in periphery. These results put forth an interesting hypothesis that, for postural control, the central retina is sensitive to both radial and translational flow, while the peripheral retina is sensitive only to translational flow. Bardy et al ((Bardy, et al. 1996, Bardy, et al. In Press)) investigating psychophysically postural responses to optic flow patterns at different eccentricities during walking found that the structure of the optic flow is more important than the retinal locus of stimulation. In particular, they found that both central and peripheral vision can use both radial

and translational flow patterns to control posture during locomotion. That radial pattern is of use in the periphery, is consistent with reports on accurate peripheral heading discrimination (Crowell and Banks 1993), and avoidance of looming objects (Stoffregen and Riccio 1990). Investigating the neural substrate for control of posture from optic flow would be very challenging with imaging or using neurophysiological recording techniques. Patients provide far more accessible a route for investigation of this issue.

When approaching a wall at a constant velocity, radial flow indicates the time of collision with the wall (Lee 1976). Local expansion and translation in the binocular array indicates that an object is approaching. Lee and colleagues, Regan and colleagues (Regan and Beverley 1979, Regan and Vincent 1995) and others have provided the behavioral data that support the role of such information in perception of time-to-contact, interceptive timing and motion-in-depth. How might we get about investigating the neural basis of such performance? Transcranial-magnetic stiumlation (TMS) provides one way in humans, but the type of tasks that could be performed is obviously constrained. Patients again offer a simple way forward. If a neurological patient loses the ability to perceive radial flow, is his/her control of locomotion impaired? If the patient has a deficit in perception of expansion can he or she still perceive motion in depth? Does a loss of sensitivity to motion in depth co-occur with impairment on postural control? Examination of the patterns of deficits of actions can tell us about the functional independence or modularity and hierarchical organization of the perceptual control of actions. Thus insight is gained into questions as to whether there is a single flow center and what role flow has in the control of actions.

Most of the questions outlined in this section wait for case study data. In the next sections we focus specifically on the perception of heading and the control of locomotion, and discuss several relevant neurological case studies.

Impairment of locomotion and recovery of locomotor function.

We (Vaina and Shepherd, in preparation) have recently studied a patient, M.Sh. an 81 years old woman who suffered a right occipital infarct in the region of the posterior cerebral artery involving the medial temporal and occipital lobes. The right cerebellum was spared. She had a left homonimous hemianopsia. Reading, colors, faces and object recognition were all normal. Her constructions in 2D and 3D were very poor, and on formal neurological examination she demonstrated some left side neglect from which she fully recovered in a few days. The patient was brought to our attention because in spite of normal vestibular and cerebellar signs, her posture and gait were off Her gait was unsteady and very slow, and when walking she was noticeably veering to the right. On a series of psychophysical motion tests she performed normally on direction discrimination in random dot kinematograms for stimuli presented in her normal field, however, her discrimination of radial flow and straight trajectory heading was severely impaired even when the stimuli were fully presented in her normal visual field. Her walking pattern is very similar to the reported behavior of patient W.V. studied by Rushton et al (1998) (Rushton, et al. 1998).

Patient W.V. is a 64-year-old male, who suffered a right temporal-parietal damage associated with left homonymous hemianopsia and hemiparesis. Immediately after the lesion, the patient exhibited marked left visual neglect, first informally noted on the ward during normal activities and then clinically assessed. For example, on the cancellation task (Albert 1973) he showed consistent left omissions, and right omissions with visual reversal. On the line-bisection task he made rightward errors. Also on copying he omitted the left side of the figure. Further details of W.V.ís neurological and neuropsychological history and some neglect testing are to be found in Shillcock, Kelly & Monaghan (Shillcock, et al. 1998). Initially his mobility was restricted, but after extended physical therapy he regained his ability to walk unaided. It was at this time that he returned for an out-patient appointment, proud to demonstrate his ability to

walk, that his wife mentioned his curved trajectories. He was able to reach objects or places of interest, he just took a strange route to get to them. Rushton (Rushton, et al. 1998) investigated W.V.ís veering motion, but an explanation for this behavior was not immediately obvious. The veering of neglect patients has been reported previously. The reports were not particularly problematic for flow theories of heading because the reports described left-sided (assuming left neglect) collisions and being "magnetically" pulled towards right doorposts. Veering while walking through an open environment is more difficult to account for.

It has been reported that some patients with neglect misperceive the "straight-ahead" direction, this can be tested by giving the patient a laser pointer and having them point to a position on a wall opposite that is directly ahead of them. Instead of pointing to the point directly ahead they may point to a position approximately 15 degrees to one side (see (Karnath 1994). As noted in a previous section, one potential walking strategy is to ignore optic flow and instead simply place an object of interest directly ahead and walk forward. Under normal circumstances this would lead to a straight trajectory toward an object of interest. However, if the observer misperceives the true straight-ahead direction then it predicts a curving trajectory that eventually reaches the object. In contrast, if optic flow guides locomotion then the misperception of the direction of straight ahead should not matter, all that is critical is the relative position of the target and the (if necessary recovered) focus of expansion.

The misperception of egocentric direction hypothesis was tested with normal subjects. The locomotion- models were pitted against each other by displacing the perceived direction of objects in normal observers with prism glasses. It was found that they took a veering trajectory when walking to a target. The trajectory was well described by the "place the target straight-ahead" model, and clearly very different to that expected from the flow-model.

To determine whether misperception of ego-centric direction could account for W.V.'s behavior, it was arranged to assess his walking trajectories on his next out-patient visit.

However, when he was tested he proceeded to walk a perfectly straight trajectory to the target given him. He was then tested with prism glasses that had been brought along to "cure" his veering. With the prisms he continued to walk a straight course. This meant that we were unable to determine if the hypothesis regarding his earlier veering was correct. However, his later behavior provides further important information. Normals do not walk straight with prisms unless they undergo a period of adaptation. W.V.'s ability to walk straight with prisms indicates that it is possible to learn new strategies for locomotion around the environment.

Heading perception in the presence of objects.

The real world environment is cluttered with stationary and moving objects that may aid or hinder heading perception. In the presence of independently moving objects it has been hypothesized that the visual motion system could (a) segment the scene using optic flow together with contrast, texture, and extra-retinal signals to remove objects from the heading estimate (Adiv 1985, Hildreth 1992, Hildreth and Royden 1998, Thompson 1993) or (b) simply pool across motion vectors to find the best-fit radial pattern. In the case of a motion pooling mechanism, this would yield systematic heading errors. (Warren and Saunders 1995) found that an object moving in depth does in fact bias perceived heading by a few degrees toward the object's center of motion, consistent with spatial pooling. In contrast, (Royden and Hildreth 1996) observed that a laterally moving object produces a heading error in the opposite direction. Although these effects are small and only occur when the object obscures the heading point (global center of motion), they suggest that the scene may not be segmented prior to heading estimation. Our data from several patients (Vaina, et al. 1994a, Vaina, et al. 1996b); Vaina &Royden,1999) appear to support this hypothesis. For example, at the time when patient R.A. (Vaina, et al. 1996b) was impaired on perceiving segmentation from motion

(Figure 1 b and d show his performance on Motion Discontinuity and on 2D-Form-from Motion Contrast) and failed to recover 3D-Structure-from-Motion, (Figure 1h), his performance on Straight-Trajectory Heading (Figure 1j) was normal. His performance on spatial integration of motion signals (the Motion Coherence test) was also normal (Figure 1h). If hypothesis (a) was correct then it would be expected that damage to a mechanism early in the perception of heading process would lead to an impairment on heading perception. The lack of impairment suggests that to discriminate radial motion and straight trajectory heading in an environment populated with objects, he might use hypothesis (b). In patients similar to R.A. it would be revealing to formally test heading in the presence of static or moving objects, by using methods similar to those used in psychophysics with normal subjects.

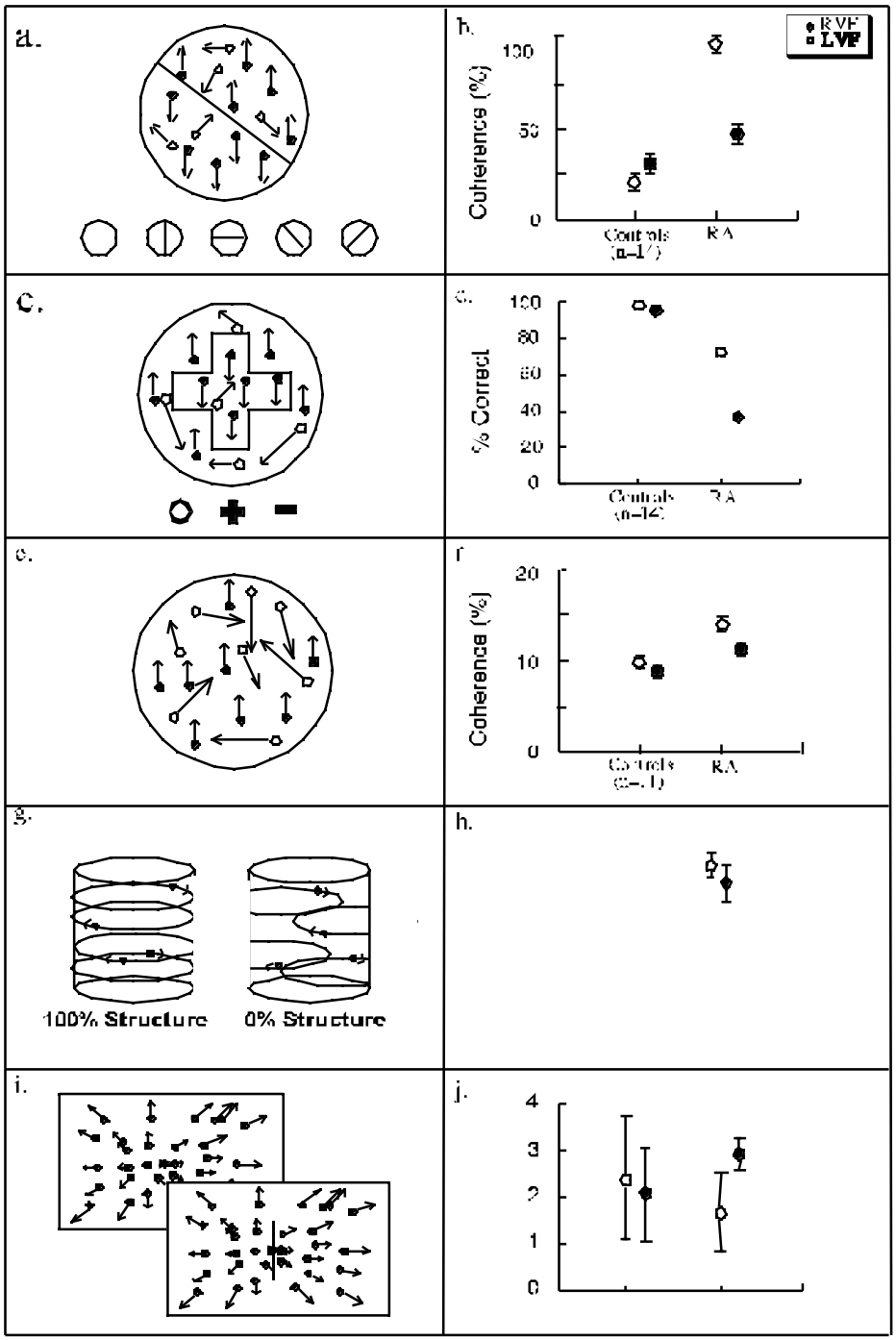

Figure 1

On top, pannels a,c,e,g and i illustrate schematic drawings of the random dot motion stimuli.. The corresponding pannels on the bottom (b,d,f,h, and j) show the data from patient R.A. and

matched control subjects. The open circle indicate data from stimuli presented in the left-visual-field, for processing with the right hemisphere; and the filled circle indicate data from stimuli presented in the right visual field. (This convention is maintained in all the figures in this chapter) **(a) Discontinuity detection**: in a single stimulus interval, the subject is asked to report whether the display is homogeneous or it contains a motion discontinuity. In the discontinuous case, half of the signal dots move upwards and the other half move downward. The figures on the bottom illustrate the types of displays, the first indicates that no discontinuity is present, and the other 4 show the orientation of the imaginary discontinuity border. The difficulty of the test is manipulated by varying according to an adaptive staircase procedure the proportion of the signal and noise dots. The signal and noise dots are defined according to the algorithm described by (Newsome and Pare 1986) and Vaina et al., 1990**.** This task is described in detail in Vaina, Grzywacz, et al, 1994**. (b)** The graph shows comparatively RA's performance and that of 14 normal control subjects. The y-axis shows the percent coherence (the coherence threshold defined as the mean of the last six reversals in the adaptive staircase) necessary for discriminating reliably discontinuity in the display. **(c) Discrimination of 2D form from motion contrast:** The display is similar to that described in (a), except that in the center of the display when the shape is present the oppositely moving signal dots either delineate an imaginary cross or an oblong. Constant stimuli were used in this task and subjects were asked to determine whether the display was honogeneous, contained a central cross or an oblong moving in opposite direction from the background. In 33% of the trials there the signal dots in the entire display move homogeneously upwads or downwards. The proportion of noise dots was fixed to 0.05 which is well in the range of RA's ability to discriminate direction of motion (as demonstrated in Pannel 1f)**;.(d)** The graph shows the performance (expressed as percent correct) of 13 normal control subjects and RA. **(e) Motion coherence:** The display is similar to that portrayed in (a), except that no discontinuity is present. The subjects' task is to discriminate

whether the motion is upwards, downwards,left or right. The proportion of signal dots was manipulated by an adaptive staircase. This exact stimulus is described in detail in Vaina, Grzywacz et al, 19994. **(f)** The graph shows the threshold (defined as the mean of the last six reversals in the adaptive staircase) expressed as percent of coherently moving dots required by normal observers and R.A. for direction discrimination. **(g) 3D Structure-from-motion** In a spatially two-alternatives forced choice task.subjects are requested to determine which of the two random dot kinematograms (top or bottom) represents a "better" transparent rotating cylinder. The dots in one of the kinematograms, the "structured" display, are the orthographic projection of points on the surface of a hollow cylinder rotating with 30deg/sec around its vertical axis. In the other kinematogram, the "unstructured" stimulus the "noise" dots that corrupt the structure of the cylinder, move with the same angular velocity along a circular trajectory of the same radius as the "signal" dots, but their rotation axis is horizontally offset by a variable amount to the left or right of the "structured" stimulus axis of rotation. **(h)** The figure illustrates thresholds from R.A. and 6 matched normal control subjects, for the discrimination of the structured display.. The Y-axis represents percent structure necessary for reliable discrimination **(i) Straight-line-heading** (courtesy of Royden) The display consists of a random dot kinematogram which simulate what an observer would see if approaching two transparent planes of dots at a distance of 400 and 1000 cm. The simulated motion of the observer is purely translation. The simulated observer's speed is 200cm/sec and its direction varies to the left or right of the center of the display. After the motion sequence dissapears, a vertical line appears at a given horizontal angle from the true heading. In a two alternative choice task and constant stimuli subjects are asked to indicate whether their heading was to the left or to the right of the vertical line. **(j)** The graph displays the heading accuracy (in degrees of visual angle) of 16 normal observers and RA.

The functional deficit experienced by patient J.V. (Vaina, Jacobs, Valder, Bienfang, Zamani, 1999) may reveal the role objects in guiding locomotion. J.V. is a 63 years old, right handed woman who had an embolic stroke, in the left occipital lobe, involving the inferior occipital gyrus. She has full visual fields by formal neuro-ophthalmological examination. On the first visit, six months after the stroke, she spontaneously reported that "I must be very careful how I walk and where I step, often I do not see a step or an object in front of me", "when I go shopping, I feel overwhelmed by people walking around me, and I seem to lose my way in a crowd where people move in different directions. But I do not have this problem when I am out there in the field".

Figure 2 shows her performance on direction (Figure 2b) and speed discrimination (Figure 2d) and on the discrimination of complex patterns of motion: translational, circular and radial (Figures 2 f,h,j). In all cases, and for stimuli shown in either visual field, her performance was not significantly different from that of the normal population (the z scores between her thresholds on these tasks and the thresholds of the age matched normal controls were less than 2).

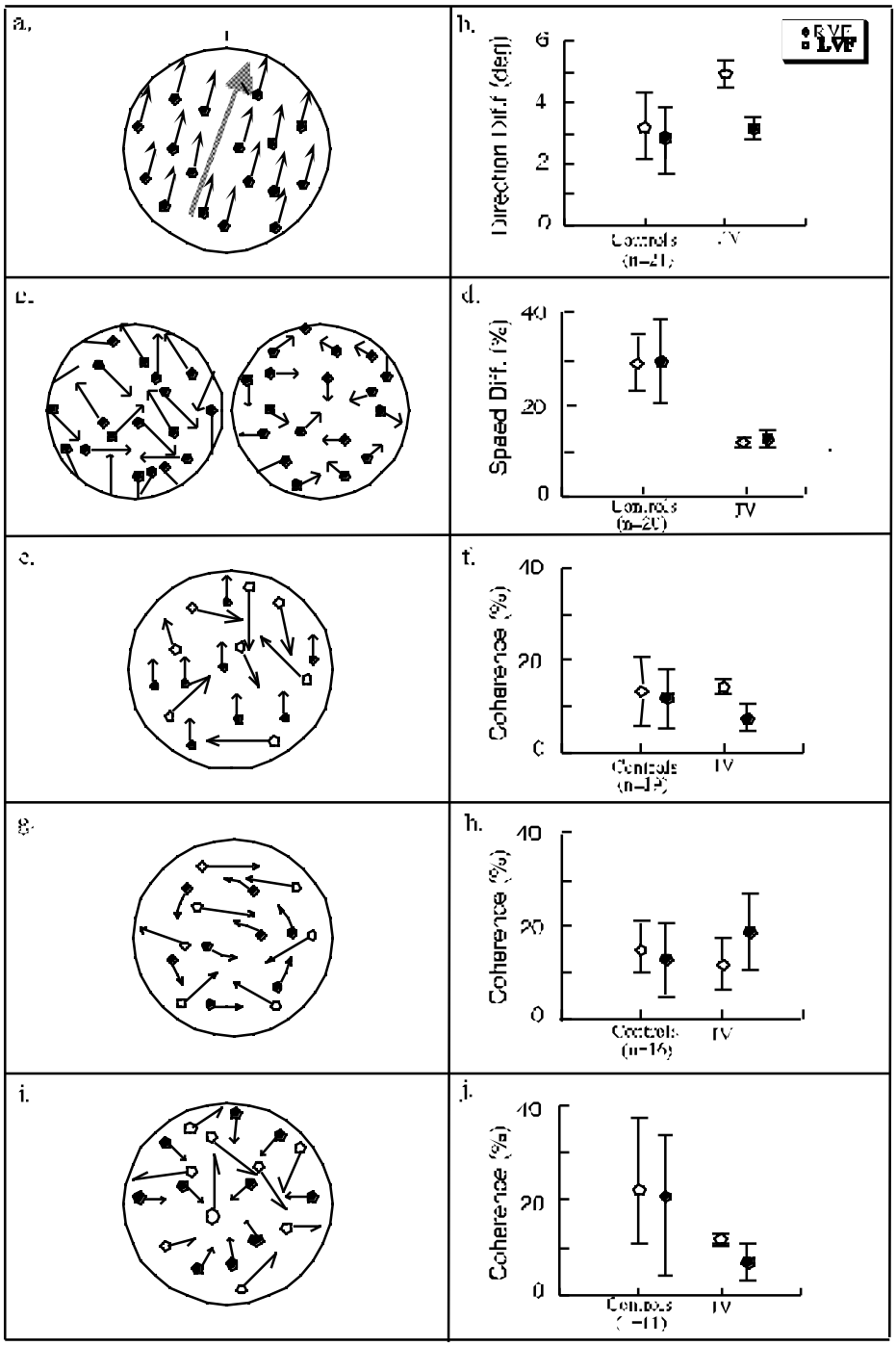

Figure 2

The top row (a,c,e,g,i) displays schematically the motion stimuli used. The graphs on the bottom show the data from normal controls and subject JV for each of these tests. . The data from the patient plotted here was obtained at 4 months after she

began coming to the laboratory (10 months after her stroke)A more detailed description of the motion tests c an be found in Vaina, Cowey., Makris and Kennedy, 1998. **(a) Direction discrimination**: The stimulus consists of a random dot kinematogram displayed in a circular aperture. In a two alternatives forced choice task subjects are asked to indicate whether the dots move to the left or to the right of an imaginary vertical line. The stimuli are displayed by an adaptive staircase procedure varying the difference (the angle) between the direction of the dots and the imaginary vertical. **(b)** The graph shows threshold on direction discrimination from 21 matched normal controls and JV**.(c) Speed Discrimination:**: Random dot kinematogram are displayed in displayed in two apertures, on above the other. Each dot trajectory changed randomly from frame to frame, but the speed was the same for all the dots within an aperture. The standard speed was presented in one aperture (randomly, top or bottom) and the test speed in the other. The standard speed was varied by an adaptive staircase procedure, and observers were asked to report in which of the two apertures the dots appeared to move faster. The test is described in detail in Vaina et al, 1990, 1998. **(d)** Data from the speed test from JV and 20 matched normal controls. The Y-axis represents the subject's threshold expressed in the percent of speed difference between the standard and test speed. **(e) Motion coherence:** The test was replicated from Newsome and Pare, 1986. A detailed description can be found in Vaina et al., 1990, 1998. The display consists of a random dot kinematogram in which a variable proportion of the dots provide directional signal (up, down, left or right) and the reminder provide masking motion noise. The proportion of signal is varied by an adaptive staircase procedure...Subjects are requested to indicate the global direction of motion. **(f)** .The graph represents the data from JV and 19 age matched normal controls. The threshold shown on the Y axis, represents the

percent coherence necessary for reliable direction discrimination of the stimulus. **(g) Circular motion:** The display is similar to the motion coherence, except that the direction of the signal dots is either clockwise or counterclockwise**.(h)** The graph shows thresholds, expressed as percent coherence, for JV and 16 matched normal controls. **(i) Radial Motion:** The stimulus is similar to e and g, except that the direction of the signal dots is either expansion or contraction (shown in the figure). The proportion of signal dots (expanding or contracting) was varied by an adaptive staircase procedure**.** **(j)** The graph shows the thresholds, expressed as percent coherence, from JV and 11 matched normal controls.

This data illustrates her performance after 4 months of weekly visits to our laboratory for evaluation and training on tasks of visual motion perception. Initially she was impaired on speed discrimination, but improved to normal level within a few weeks.

However, her performance on a Straight-Trajectory Heading task and on 3D-Structure from Motion shown in Figure 3 (b and d) remained significantly impaired, compared with the normal controls. Specifically, her performance did not change during the 9 months of weekly testing with these tasks. It is interesting, however, that the patient's self perception of her own abilities was that they improved.

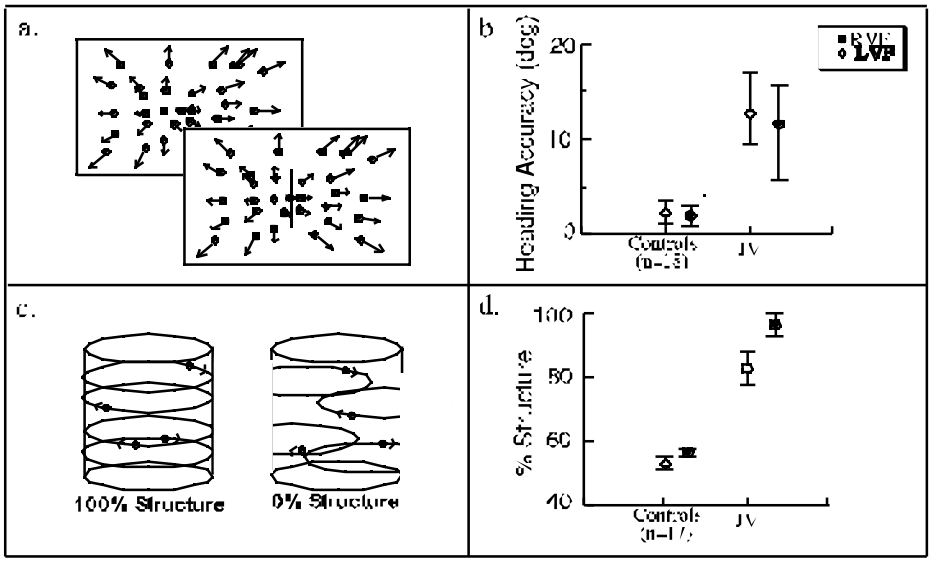

Figure 3

(a) Straight-line-heading The stimulus and the task are described in **Figure 1i. (b)** The graph displays the heading accuracy (in degrees of visual angle) of 18 normal observers and J.V.. **(c)** The stimulus and the task are described in **Figure 1 g**. **(d)** The figure illustrates thresholds from J.V. and 17 matched normal control subjects, for the discrimination of 3D structure from motion (indicate the structured display).

She began driving, but noted that this was possible only in very familiar environments, where she was aware and could "predict" all the landmarks. She still did not feel comfortable driving in novel environments. First, it is remarkable that she could drive, second it is surprising that she can even walk around. So, how could she control locomotion on foot given that she is not sensitive to the direction of flow? We noted above that the relative movement of objects in the scene provides information about direction of heading, second the egocentric direction of a target object may be used. J.V. could potentially be relying on either of these sources of information, sensitivity to which may not be impaired. Thus her behavior and performance on the psychophysical tests provide evidence against the sole use of the velocity field.

A second problematic case for velocity field based models is the patient G.Z. (Vaina, et al. 1999c). She showed a clear -cut dissociation between normal judgment of heading when familiar landmarks are present in the display (a simulate room) and the complete failure to perceive heading in dynamic random dot stimuli. First as we noted at the beginning of this chapter, natural scenes contain continuous surfaces and dynamic occlusions at depth edges, which computationally could simplify the determination of heading direction. This itself may account for G.Z.'s dissociation. However, the landmark display contained salient features and reference objects that can be tracked over time. The patient's account of how she made the decision about her heading, revealed that she was tracking the visibility of the reference objects (objects of furniture). This suggests that she may be using one of the alternatives to the velocity filed, the egocentric target direction or relative motion of objects in the perception of the direction of locomotion. An interesting question arises, can we find the reciprocal case: patients that are sensitive to radial flow but topographically disoriented, i.e. impaired on spatial relationships between (a) objects in the environment or (b) objects and themselves, that can successfully locomote around the environment?

Two recent studies of (Cammalleri 1996, Takahashi, et al. 1997) described patients with lesions involving the posterior cingulate cortex, who do not have either of the above spatial deficits, they are both able to recognize landmarks and to relate to objects in the environment, but they have selectively lost their heading discrimination ability, as they cannot derive directional information from the landmarks they recognize. As pointed out by Aguirre et al (Aguirre, et al. 1998) the posterior cingulate cortex in rodents contains head-direction cells, and they appear to fire to a combination of ego-motion, landmark and vestibular cues.

We have described several patients that exhibit behavior that is problematic for the velocity field account of heading. None of the studies are conclusive, but they are suggestive

and we have demonstrated or discussed how the hypotheses they provoke can be tested with normal subjects, further testing of patients with similar deficits or patients with the opposite pattern of behavior.

Conclusion

In this chapter we have highlighted two related issues: does optic flow guide locomotion (and if so which features of the flow field), and what else is flow used for (eg postural control, interceptive timing etc)? These points raise questions such as, if optic flow is used to guide locomotion, postural control, interceptive timing etc then is there a single 'flow system', or a number of specialized systems or routes, if object displacement is used to guide natural locomotion then what neural areas are implicated in the necessary processing? Studying neurological patients allows us to get some early and important insights into these matters. Case studies naturally complement standard psychophysical experiments, manipulations or perturbations of behaviors in natural environments, precise neurophysiology and computational modeling. However, lesions in human patients are not always where one would like them to be and there are complicating factors which must be addressed (e.g. functional damage is often not restricted to the lesioned area as retrograde synaptic degeneration (Sachdev, et al. 1990) or diaschisis (Feeney and Baron 1986) may functionally affect brain areas that anatomically, on structural imaging studies appear intact). However, their primary value can be summed up as: if we listen to what patients tell and note their behavior then they will teach us what we didn't expect, that we wouldn't predict and can't explain! In such a well-developed incrementally progressing research area as optic flow this is an invaluable contribution. Early and tentative conclusions derived from patient work suggest that it is important to reestablish the validity of many assumptions and priorities associated with research on optic flow.

Acknowledgments

The preparation of this manuscript LMV was supported by a National Institute of Health grant EY-2RO1-0781 and SKR was supported in part by a grant from the UK MRC and by Nissan Research and Development Inc. We thank Alan Cowey, Mark Bradshaw, Franco Giuliannini for valuable comments and Damien Henderson for drawing the figures and help with formatting the manuscript.

REFERENCES

Adiv, G. (1985). Determining three-dimensional motion and structure from optical flow generated by several moving objects. IEEE Pattern Analysis and Machine Intelligence. **7:** 384-401.

Aguirre, G. K., Zarahn, E. and D'Esposito, M. (1998). Neural components of topographical representation. Proceedings Of The National Academy Of Sciences Of The United States Of America. **95:** 839-46.

Albert, M. I. (1973). A simple test of visual neglect. Neurology. **23:** 658-664.

Ambland, B. and Carblanc, A. (1980). Role of foveal and peripheral vision information in the maintenance of posture equilibrium in man. Perceptual and Motor Skills. **51:** 903-916.

Andersen, G. J., & Dyre, B. P. (1989). Spatial orientation from optic flow in the central visual field. Perception and Psychophysiology. **45:** 453-458.

Andersen, R. A. (1990). Visual and Eye Movement Functions of the Posterior Parietal Cortex. Ann. Rev. Neurosci. **12:** 377-403.

Andersen, R. A. (1997). Neural Mechanisms of visual Motion Perception in Primates. Neuron. **18:** 865-872.

Andersen, R. A., Bradley, D. C. and Shenoy, K. V. (1996). Neural mechanisms for heading and structure-from-motion perception. Cold Spring Harbor Symposia on Quantitative Biology, Cold Spring Harbor Lab. Press.

Andersen, R. A., Snyder, L. H., Bradley, D. C. and Xing, J. (1997). Multimodal Representation of Space in the Posterior Parietal Cortex and its use in Planning Movements. Annu. Rev. Neurosci. **20:** 303-330.

Bardy, B., Warren, W. J. and Kay, B. (1996). Motion parallax is used to control postural sway during walking. Exp. Brain Res. **111:** 271-282.

Bardy, B. G., Warren, W. H. and Kay, B. A. (In Press). The role of central and peripheral vision in postural control during woring. P&P.

Beauchamp, M. and DeYoe, E. (1996). fMRI of human parietal and occipital areas for processing visual motion and their graded modulation by spatial and featural attention. Soc. Neurosci. Abstr. **26:** 1198.

Britten, K. H. and van Wezel, R. J. A. (1998). Electrical microstimulation of cortical area MST biases heading perception in monkeys. Nat Neurosci. **1:** 59-63.

Cammalleri, R. (1996). Transient topographical amensia and cingulate cortex damage:a case report. Neuropsychologia. **34:** 321-326.

Cheng, K., Fujita, H., Kanno, I., Mura, S. and Tanaka, K. (1995). Human Cortical Regions Activations by Wide Field Visual Motion : An H215O PET Study. J. Neurophy. **74:** 413-426.

Clifford, C. W. G. and Vaina, L. M. (1998). A computational model of selective deficits in first- and second-order motion perception [ARVO Abstract]. Invest Ophthalmol Vis Sci. **39:** S1077. Abstract nr 4982.

Crowell, J. A. and Banks, M. S. (1993). Perceiving heading with different retinal regions and types of optic flow. Perception and Psychophysics. **53:** 325-337.

Cutting, J. E. (1986). Perception with an Eye Towards Motion. Cambridge, MA, MIT Press.

Cutting, J. E., Springer, K., Braren, P. A., & Johnson, S. H. (1992). Wayfinding on foot from information in retinal, not optical, flow. J Exp Psy: General. **121:** 41-72.

Dale, A., Ahlfors, S. P., Aronen, H. J., Belliveau, J. W., Huotilainen, M., Ilmoniemi, R. J., Kennedy, W. A., Korvenoja, A., Liu, A. K., Reppas, J. B., Rosen, B. R., Sereno, M. I., Simpson, G. V., Standertskjold-Nordenstam, C.-G., Virtanen, J. and Tootell, R. B. H. (1995). Spatiotemporal Imaging of Coherent Motion Selective Areas in Human Cortex. Society for Neuroscience, San Diego, CA.

Dale, J., Dale, A., Liu, A., Rosen, B. and Tootell, R. (in revision). The representation of visual motion in human dorsal stream.

Duchon, A. P. and Warren, W. H. (1998). Interaction of two strategies for controlling locomotion [ARVO Abstract]. Invest Opthalmol Vis Sci. **39:** S892. Abstract nr 4122.

Duffy, C. J. and Wurtz, R. H. (1996). Optic flow, posture and the dorsal visual pathway. Perception, Memory and Emotion: Frontier in Neuroscience. T. Ono, B. McNaughton, S. Molotchnikoff, E. Rolls and H. Nishijo, Elsevier Science, Oxford, NY, Tokyo**:** 63-77.

Duhamel, J. R., Bremmer, F., BenHamed, S. and Graf, W. (1997). Spatial invariance of visual receptive fields in parietal cortex neurons. Nature. **389:** 845-8.

Dupont, P., De Bruyn, B., Vandenberghe, R., Rosier, A., Michiels, J., Marchal, G., Mortelmans, L. and Orban, G. A. (1997). The kinetic occipital region in human visual cortex. Cereb Cortex. **7:** 283-292.

Dupont, P., Orban, G. A., Bruyn, B. D., Verbruggen, A. and Mortelmans, L. (1994). Many areas in the human brain respond to visual motion. J. Neurophysiol. **72:** 1420-1424.

Feeney, D. M. and Baron, J. C. (1986). Diaschisis. Stroke. **17:** 817-830.

Gegenfurtner, K., Kiper, D. and Levitt, J. (1997). Functional Properties of Neurons in Macaque Area V3. Journal of Neurophysiology?**:** 1906-1923.

Greenlee, M. W. and Smith, A. T. (1997). Detection and discrimination of first- and second-order motion in patients with unilateral brain damage. J.Neuroscience. **17:** 804-818.

Hildreth, E. C. (1992). Recovering heading for visually-guided navigation. Vision Res. **32:** 1177-1192.

Hildreth, E. C. and Royden, C. S. (1998). Computing Observer Motion from Optical Flow. High-Level Motion Processing: Computational, Neurobiological, and Psychophysical Perspectives. T. Watanabe. Cambridge, MA, MIT Press**:** 269-293.

Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. Perception & Psychophysics. **14:** 201-211.

Karnath, H. (1994). Subjective body orientation in neglect and the interactive contribution of neck muscles and proprioception and vestibular stimulation. Brain. **117:** 100-112.

King, S. M., Frey, S., Villemure, J. G., Ptito, A. and Azzopardi, P. (1996). Perception of motion-in-depth in patients with partial or complete cerebral hemispherectomy. Behavioural Brain Research. **76:** 169-80.

Koch, C., Wang, H. T. and Mathur, B. (1989). Computing Motion in the Primate's Visual System. J. exp. Biol. **146:** 115-139.

Lee, D. N. (1974). Visual information during locomotion. Perception: Essays in Honor of James Gibson. R. B. Macleod and H. Pick. Ithaca, NY, Cornell University Press.

Lee, D. N., & Lishman, J. R. (1975). Visual proprioceptive control of stance. Journal of Human Movement Studies. **1:** 87-95.

Lee, D. N. (1976). A theory of visual control of braking based on information about time-to-collision. Perception. **5:** 437-459.

Llewellyn, K. R. (1971). Visual guidance of locomotion. J Exp Psychol. **91:** 245-261.

Marcar, V. L., Zihl, J. and Cowey, A. (1997). Comparing the visual deficits of a motion blind patient with the visual deficits of monkeys with area MT removed. Neuropsychologia. **35:** 1459-1465.

Maunsell, J. H. and Essen, D. C. V. (1983a). Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed, and orientation. J. Neurophysiol. **49:** 1127-1147.

Maunsell, J. H. R. and Essen, D. C. V. (1983b). The connections of the middle temporal visual area (MT) and their relationship to a cortical heirarchy in the macaque monkey. J. Neurosci. **3:** 2563-2586.

McLeod, P., Dittrich, W., Driver, J., Perret, D. and Zihl, J. (1996). Preserved and impaired detection of structure from motion by a "motion blind" patient. Visual Cognition. **3:** 363-391.

Nakayama, K. (1985). Biological image motion processing: A review. Vision Research. **25**.

Nakayama, K. (1994). James J. Gibson -- An Appreciation. Psychol Rev. **101:** 329-335.

Newsome, W. T. and Pare, E. B. (1986). MT lesions impair discrimination of direction in a stochastic motion display. Soc. Neurosci. Abstr. **12:** 1183.

Plant, G. T., Laxer, K. D., Barbaro, N. M., Schiffman, J. S. and Nakayama, K. Impaired visual motion perception in the hemifield contralateral to unilateral posterior cerebral lesions in humans, Smith Kettlewell Eye Research Institute, University of California at San Francisco, and Letterman Army Medical Center.

Pollen, D. A. (1999). On the neural correlates of visual perception. Cerebral Cortex. **9:** 4-19.

Read, H. L. and Siegel, R. M. (1997). Modulation of Responses to Optic Flow in Area 7a by Retinotopic and Oculomotor Cues in Monkeys. Cerebral Cortex. **7:** 647-661.

Regan, D. and Beverley, K. I. (1979). Visually Guided Locomotion: Psychophysical Evidence for a Neural Mechanism Sensitive to Flow Patterns. Science. **205:** 311-313.

Regan, D. and Vincent, A. (1995). Visual processing of looming and time to contact throughout the visual field. Vision Research. **35:** 1845-57.

Riddoch, G. (1917). Dissociation of Visual Perceptions Due to Occipital Injuries With Especial Reference to Appreciation of Movement. Brain. **40:** 15-57.

Royden, C. and Hildreth, E. (1996). Human Heading Judgments in the Presence of Moving Objects. Perception and Psychophysics. **58:** 836-856.

Rushton, S. K., Harris, J. M., Lloyd, M. R. and Wann, J. P. (1998). Guidance of locomotion on foot uses perceived target location rather than optic flow. Current Biology. **8:** 1191-4.

Sachdev, M., Kumar, H., Jain, A., Goulatia, R. and misra, N. (1990). Transsynaptic neuronal degeneration of optic nerves associated with bilateral occipital lesions. Indian Journal of Ophthalmology. **38:** 151-152.

Schaafsma, S. J., Duysens, J. and Gielen, C. C. (1997). Responses in ventral intraparietal area of awake macaque monkey to optic flow patterns corresponding to rotation of planes in depth can be explained by translation and expansion effects. Visual Neuroscience. **14:** 633-46.

Shillcock, R., Kelly, M. and Monaghan, P. (1998). Processing of plaindromes in negelct dyslexia. Neuroreport**:** 3081-3083.

Shipp, S., de Jong, B. M., Zihl, J., Frackowiak, R. S. J. and Zeki, S. (1994). The brain activity related to residual motion vision in a patient with bilateral lesions of V5. Brain. **117:** 1023-1038.

Siegel, R. and Read, H. (1997). Analysis of Optic Flow in the Monkey Parietal Area 7a. Cerebral Cortex**:** 327-346.

Srinivasan, M. V., Lehrer, M., Kirchner, W. and Zhang, S. W. (1991). Range perception through apparent image speed in freely-flying honeybees. Vis Neuroscience. **6:** 519-535.

Stoffregen, T. A. (1985). Flow structure versus retinal location in the optical control of stance. Jnal of Exp. Psychology: Human Perception and Performance. **11:** 554-565.

Stoffregen, T. A. (1986). The role of opticla velocity in the control of stance. Perception&Psychophysics. **39:** 355-360.

Stoffregen, T. A. and Riccio, G. E. (1990). Response to optical looming in the retinal center and periphery. Ecological Psychology. **2:** 251-274.

Takahashi, N., Kawamura, M., Shiota, J., Kasahata, N. and Hirayama, K. (1997). Pure topographic disorientation due to right retrosplenial lesions. Neurology. **49**.

Thompson, W. B., Lechleider, P., & Stuck, E. R. (1993). Detecting moving objects using the rigidity constraint. IEEE Patt A. **15:** 162-165.

Tootell, R., Dlae, A., Mendola, J., Reppas, J. and Sereno, M. (1996). FMRI analysis of human visual cortical area V3A. NeuroImage. **3:** S358.

Tootell, R., Reppas, J., Dale, A., Look, R., Malach, R., Jiang, H.-J., Brady, T. and Rosen, B. (1995a). Visual motion aftereffect in human cortical area MT/V5 revealed by functional magnetic resonance imaging. Nature. **375:** 139-141.

Tootell, R., Reppas, J. B., Malach, R. and al, e. (1994). Functional MRI of human V5/MT correlates with two different visual illusions. Soc. Neurosci. Abstr. **20:** 250-255.

Tootell, R. B., Mendola, J. D., Hadjikhani, N. K., Ledden, P. J., Liu, A. K., Reppas, J. B., Sereno, M. I. and Dale, A. M. (1997). Functional analysis of V3A and related areas in human visual cortex. J Neurosci. **17:** 7060-7078.

Tootell, R. B. H., Kwong, K. K., Belliveau, J. W., Baker, J. R., Stern, C. E., Hockfield, S. J., Breiter, H. C., Born, R., Benson, R., Brady, T. J. and Rosen, B. R. (1993a). Mapping Human Visual Cortex: Evidence from Functional MRI and Histology. Investigative Opthalmology and Visual Science. **34:** 813.

Tootell, R. B. H., Kwong, K. K., Belliveau, J. W., Baker, J. R., Stern, C. S., Savoy, R. L., Breiter, H., Born, R., Benson, R., Brady, T. J. and Rosen, B. R. (1993b). Functional MRI

(fMRI) Evidence for MT/V5 and Associated Visual Cortical Areas in Man. Society for Neuroscience 23rd Annual Meeting, Washington, D.C., Soc. Neuro., Wash D.C.

Tootell, R. B. H., Reppas, J. B., Kwong, K. K., Malach, R., Born, R. T., Brady, T. J., Rosen, B. R. and Belliveau, J. W. (1995b). Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. J. Neuroscience. **15(4):** 3215-3230.

Tootell, R. B. H., Reppas, J. B., Kwong, K. K., Malach, R., Born, R. T., Brady, T. J., Rosen, B. R. and Belliveau, J. W. (1995c). Functional Analysis of Human MT and Related Visual Cortical Areas using Magnetic Resonance Imaging. J Neurosc. **15:** 3215-3230.

Ungerleider, L. G. and Desimone, R. (1986). Cortical Projections of Visual Area MT in the Macaque. JCN. **248:** 147-163.

Vaina, L., Gryzwac, N., M, L. and Bienfang, D. (1994a). Selective deficits of motion integration and segregation mechanisms with unilateral extrastriate brain lesions. Investigative Ophthalomology and Visual Science. **35:** 1438.

Vaina, L., Grzywacz, N., LeMay, M., Bienfang, D. and Wolpow, E. (1998a). Perception of Motion Discontinuity in Patients with Selective Motion Deficits. High-Level Motion Processing

Computational, Neurobiological, and Psychophsyical Perspectives. T. Watanbe. Cambridge, Ma, MIT Press.

Vaina, L. M. and Cowey, A. (1996). Selective deficits to first or second order motion in stroke patients provides further evidence for separate mechanisms. **22:** 1718.

Vaina, L. M., Cowey, A. and Kennedy, D. (1999a). Perception of first- and second-order motion:

separate neurological mechanisms. Human Brain Mapping. **7:** 67-77.

Vaina, L. M., Gross, C. and Zamani, A. (1999b). Impaired recogniton of bilogical motion in patients with temporal lobe lesions. (submitted).

Vaina, L. M., Grzywacz, N., Choi, A., LeMay, M. and Beinfang, D. C. (1990a). Selective Deficits of Measurement and Integration of Motion in Patients with Lesions Involving the Visual Cortex. Invest. Opthalmol. Vis. Sci. **31:** 523.

Vaina, L. M., Grzywacz , N. M. and Kikinis, R. (1994b). Segregation of computation underlying perception of motion discontinuity and coherence. NeuroReport. **5:** 2289-2294.

Vaina, L. M., Jakab, M., Beardsley, S. and Zamani, A. (1999c). Impaired complex motion perception in patients with bilateral posterior parietal lesions [ARVO Abstract]. Invest Ophthalmol Vis Sci. **40:** S765. Abstract nr 4042.

Vaina, L. M., LeMay, M., Bienfang, D. C., Choi, A. Y. and Nakayama, K. (1990b). Intact "biological motion" and "structure from motion" perception in a patient with impaired motion mechanisms: a case study. Visual Neuroscience. **5:** 353-369.

Vaina, L. M., Makris, N. and Cowey, A. (1996a). The neuroanatomical damage producing selective deficits of first or second order motion in stroke patients provides further evidence for separate mechanisms. NeuroImage. **3:** 360.

Vaina, L. M., Makris, N., Kennedy, D. and Cowey, A. (1998b). The selective impairment of the perception of first-order motion by unilateral cortical brain damage. Vis Neurosci. **15:** 333-48.

Vaina, L. M., Royden, C. S., Bienfang, D. C., Makris, N. and Kennedy, D. (1996b). Normal perception of heading in a patient with impaired sturcture-from-motion [ARVO Abstract]. Invest Ophthalmol Vis Sci. **37:** S137. Abstract nr 2360.

Warren, W. (1999). Visually Controlled Locomotion, 40 Years Later. Ecological Psychology. **10:** 177-219.

Warren, W., Blackwell, A., Kurtz, K., Hatsopoulos, N. and Kalish, M. (1991). On the sufficiency of the velocity field for perception of heading. Biol. Cybern. **65:** 311-320.

Warren, W. H. J. and Saunders, J. A. (1995). Perceiving heading in the presence of moving objects. Perception. **24:** 315-31.

Zihl, J., Baker, C. L., Jr. and Hess, R. H. (1989). The "Motion-Blind" Patient: Low-Level Spatial and Temporal Filters. J. Neurosci. **9:** 1628-1640.

Zihl, J., Cramon, D. V., Mai, N. and Schmid, C. (1991). Disturbance of movement vision after bilateral posterior brain damage. Brain. **114:** 2235-2252.

Zihl, J., Van Cramon, D. and Mai, N. (1983). Selective Disturbance of Movement Vision After Bilateral Brain Damage. Brain. **106:** 313-340.