The Role of MSTd Neurons in Visually Guided Navigation

Thesis by

Marsha A. Maxwell

In Partial Fulfillment of the Requirements

for the degree of

Doctor of Philosophy

California Institute of Technology

Pasadena, California

1998

(Submitted on December 2, 1997)

©1998
Marsha Maxwell
All rights reserved

For my family

Contents

Abstract 1

Chapter 1 Introduction 4

PART I: VISUALLY GUIDED NAVIGATION 10

Chapter 2 Optic Flow 13

Introduction to optic flow 14

Formal Analysis of the Optic Flow Field 17

Computational Heading Estimation Models 20

Retinal Image Models 21

Discrete and Least Squares Estimation Models 22

Differential Invariance and Differential Image Motion 24

Dynamic Model and Flow Asymmetry 28

Extra -Retinal Models 29

Chapter 3 Human Visual Perceptions of Heading 32

Ego-motion from Optic Flow 35

Translation 37

Translation and Rotation 40

Chapter 4 MSTd: Anatomy, Physiology, and Function **47**

Anatomy 50

Physiology 51

MSTd and Optic Flow 62

Functional Role(s) of MSTd 68

PART II : MSTd AND HEADING PERCEPTION **69**

Chapter 5 Mechanisms of Heading Perception in Primate Visual Cortex **72**
(Portions of this chapter have appeared in print.)

Chapter 6 Comparisons of Eye Pursuit Effects on Human Perceptions of Expanding and Rotating Motion Patterns **87**

Introduction 89

Subjects 92

Instrumentation 92

Stimuli 93

Experiments 93

Results 94

Discussion 98

Conclusions 100

Chapter 7 Conclusion **102**

BIBLIOGRAPHY **109**

Appendix A: Spiral Space Adjust A-1

Appendix B: Spiral Space Quest B-1

ABSTRACT

When we move forward in the world, what we see appears to expand. It has been postulated that the focus of this expanding optic flow pattern is used to determine our direction of heading. This is only true if our eyes are still. If we move our eyes to track objects in our environment, this disrupts the retinal image and shifts the focus away from the heading. In order to recover heading, our brains must compensate for this shift. Neurons in primate cortical area MSTd respond to optic flow patterns and a portion shift their selectivity during tracking eye movements in a way that compensates for the retinal focus shift. These neurons appear to be taking into account the effects of eye movements on what we see as we navigate through the world.

When we view an expanding or rotating stimulus, the laminar motion caused by eye movements shifts the center of the retinal motion pattern in the direction of the eye movement (expansions) or perpendicular to the eye movement (rotations). Our early results indicated that expansion- and rotation-selective neurons in area MSTd of the macaque use an extra-retinal signal (efference copy or proprioception) to compensate for the shift in the retinal motion focus caused by pursuit eye movements. The second half of the thesis compares human abilities to compensate for the effects of eye movements using similar expanding and rotating patterns of random dots. Here we found that humans also made perceptual errors in localizing motion foci. Two psychophysical procedures were used, a stepwise method of adjustment (n=5) and a variant of the QUEST maximum-likelihood estimator (n=3). The extent of

compensation varied from 51-182%, (mean 105%) with expanding patterns and 22-54%, (mean 40%) with rotating patterns. Every observer demonstrated better performance (on average by a factor of 2.6) with expansions than rotations. This finding is interesting in that rotation-selective MSTd cells demonstrate a similar degree of compensation to expansion selective cells (both by ~ 42%). It is possible that the differences between human perceptions of expanding versus rotating patterns may reflect differences in the relative numbers of expansion- and rotation-selective cells.

CHAPTER :1
Introduction



- Tom DeClue

Night reveals many secrets in the sky that are hidden from us during the day inspiring many imagined and real adventures throughout history. Closer to home, neuroscientists are "watching" and "listening" to the brain which by some estimates houses as many neurons as stars in the galaxy. It is quite possible that after we have thoroughly explored our solar system, we will find that the brain is the final frontier.

1

As we look out into the night it is hard to believe that we hold in our heads as many cells as stars in the galax. It is even harder to imagine that these billions of cells form their own constellations of sights and sounds, movements and memories. From the moment of our conception, we are bombarded with information about the world around us whether that be chemical changes telling the cell it is time to divide or, later in our development, to differentiate into cells that subserve language or distinguish fragrances. It is the aggregation of these signals and sensations in varying brain areas that educates our minds about the world around us. Somewhere somehow this unyielding stream of information is transformed from electric and chemical signals into our concepts of morality, truth, justice, and love. It compels some to be great dancers or eloquent speakers, others to be criminally minded, and still others to prefer strawberry over chocolate. In essence this 31/2 pound galaxy that we carry in our heads defines us collectively as human beings and determines for each of us what it means to be human.

From our vantage point here on earth, the universe appears large and complex. To put order to the movement of the planets, astronomers like Kepler, Galileo, and Newton established that planets moved in ellipses and that this motion was caused by the gravitational pull exerted by the sun. In doing so they were able to first explain and then predict the macroscopic behavior of their universe from fundamental principles. Modern neuroscientists faced with the Herculean task of unraveling the mysteries of the brain are not unlike these early astronomers and physicists who tackled problems in celestial mechanics. Neuroscience attempts to rationalize macroscopic human behavior by analyzing smaller, more fundamental parts of the brain. This thesis characterizes one of these fragments - the dorsal portion of the medial superior temporal area- MSTd -- and explains how the activity of neurons in this small part of the macaque brain are related to the behavioral act of self navigation.

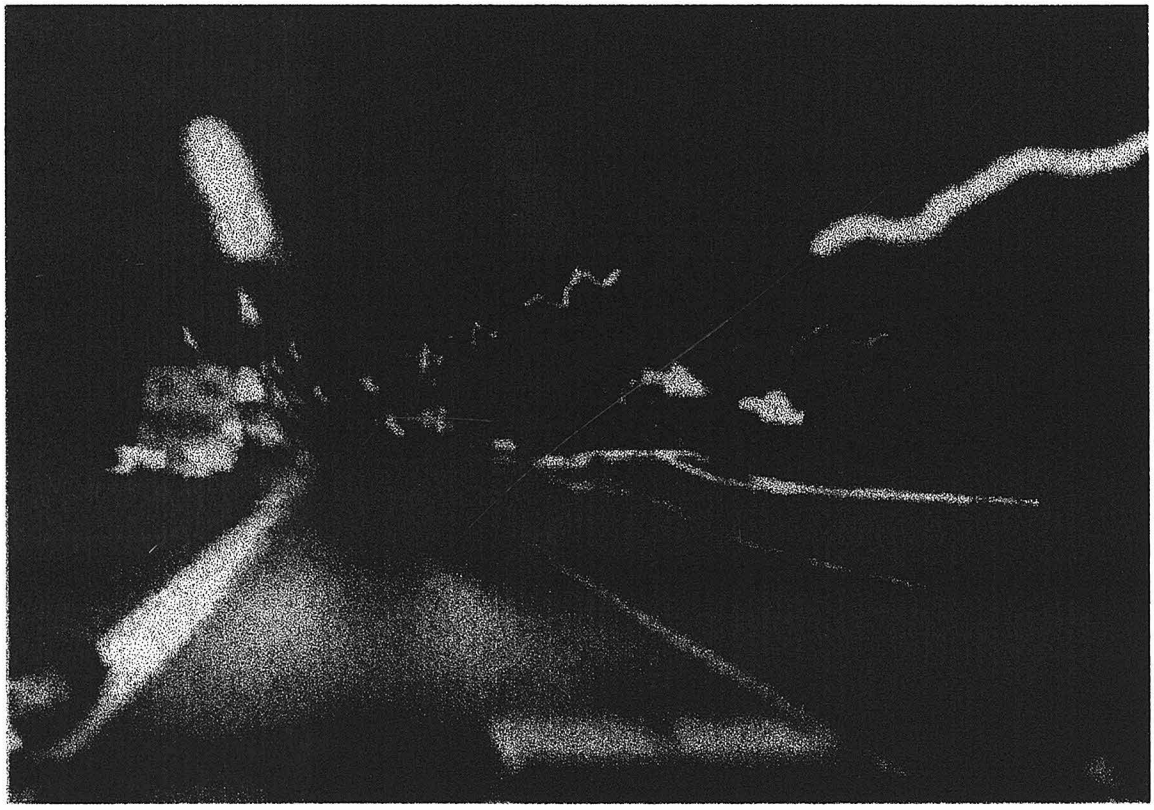
At the most basic behavioral level, we must differentiate our movements from those of objects in view. In order to survive we must effectively utilize this visual information. How we guide our motion is linked to this fundamental psychological question of how we perceive motion in the three dimensional visual world that surrounds us. It is believed that we navigate by exploiting optic flow signals. These expanding, rotating and spiraling patterns arise when we make simple and complex movements and are complicated when we make eye movements to track objects in our visual field. The purpose of this thesis is to first determine whether MSTd has a role in interpreting these optic flow

signals for the purposes of heading estimation and how its responses to these stimuli are modified when we move our eyes.

This thesis ties together three major strands of previous work. It has as its foundations the computational aspects of optic flow, early human psychophysical studies of ego motion and heading estimation as they relate to optic flow, and finally previous explorations into the physiological capabilities of area MSTd. **Part I: Visually Guided Navigation**, begins by giving an overview of the theoretical aspects of navigation in **Chapter 2- Heading from Optic Flow Information.** Here we are concerned with obtaining navigation information from optic flow fields. By the end of Part 1, a fundamental understanding of the computational theories associated with navigation will have been presented along with the problems that arise when presenting theoretical vision systems with realistic environments and biological constraints. **Chapter 3- Human Visual Perceptions of Heading**, is primarily a review of earlier work highlighting the ability of human subjects to receive reliable heading information from optic flow signals. This chapter closes with what is required of the physiological area(s) that could support the perception of ego-motion in primates. The last chapter in this portion of the thesis is **Chapter 4 - MSTd: Anatomy, Physiology and Function**, which gives a complete history of relevant physiological work done in area MSTd. .

Part 2: The Role of MSTd Neurons in Visually Guided Navigation, begins with a description of our search for the center of navigation in MSTd.

Chapter 5 - Mechanisms of Heading Perception in Primate Visual Cortex, is based in large part on recently published results and details the methods we used to determine whether or not MSTd is involved in ego motion with or with eye movement signals. Finally, we explore the links between the activity of macaque MSTd neurons and human perceptions of heading in **Chapter 6- A Comparison of Eye Pursuit Effects on Human Perceptions of Expanding and Rotating Motion Patterns**.



-Takeshi Iwasaki

This time lapse photograph captures the motion observed by a commuter. The lights streamming away from a common point in the scene are reminiscent of optic flow lines. It has been shown that observers use optic flow cues to determine their heading. At some point he will undoubtably make an eye movement to check the course of the truck in the next lane. Can he still determine his heading while moving his eyes? What strategies are available to his brain to counter this eye movement? Where in the primate brain could these computations be taking place?

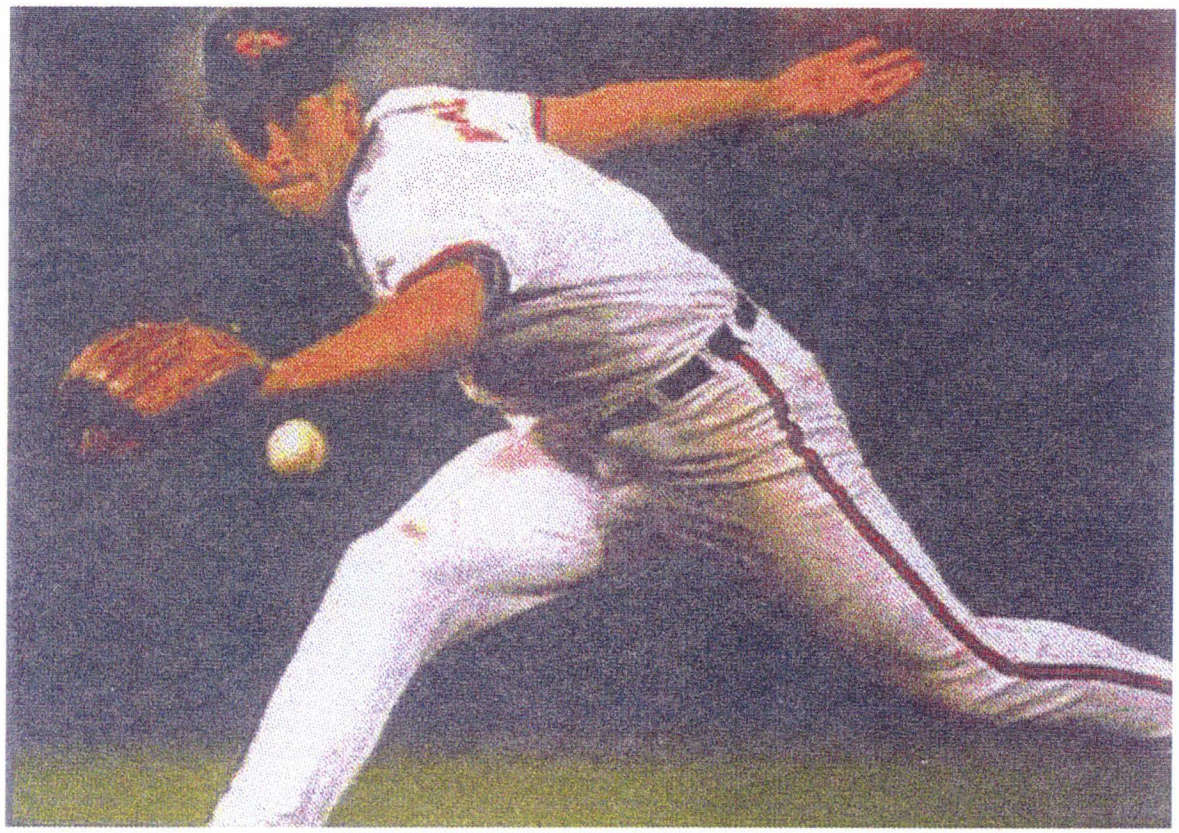
Part I: Visually Guided Navigation

Chapter Two:
Heading from Optic Flow Information

Chapter Three:
Human Visual Perceptions of Heading

Chapter Four:
MSTd: Anatomy, Physiology, and Function

Chapter 2:
Heading from Optic Flow Information



-Sports Illustrated

Professional athletes have extra-ordinary hand-eye and body coordination. How is this baseball player able to use the information on his retina to guide his movements in order to successfully intercept the ball?

2

The baseball player seems to effortlessly catch the line drive. The whole exercise takes just seconds, but in that time his brain makes the many calculations that allow him to first determine the trajectory of the ball, adjust his approach speed, and finally move his gloved hand to intersect it. In order to make the catch the athlete must successfully utilize information about his environment- the slant of the playing field, the speed and the initial direction of the ball, gathered by his visual system. In this example we see in practice the visual control of self motion. For the past century we have been trying to determine just what elements found in the visual environment allows this athlete's brain to extract information that can be used to control his motion. This chapter is primarily concerned with the theory and the computational models that attempt to explain how our brains use information derived from optic flow for navigation.

Optic Flow

When an observer moves about in a rigid* three dimensional environment, a flow of motion occurs on the retina. This motion pattern is what is commonly referred to as optic flow#. *Figure 1* shows the optic flow field that is generated by an observer moving parallel to a ground plane.[1] James Gibson, a perceptual psychologist, was one of the first to propose that this optic flow field is an important tool for navigation. It can provide information about the 3-D structure of the environment for both stationary and moving observers, the distance of objects in the visual field, the spatial arrangement of the objects viewed by the observer and the rate of change of this arrangement.[2,3,4]

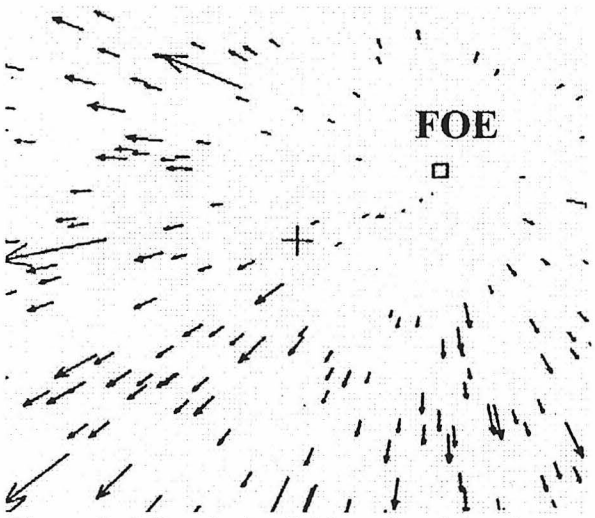


Figure 1: 2-D velocity field produced by observer motion through a rigid 3-D environment. The focus of expansion (FOE), denoted by a small square, marks the observers destination point or heading when the eyes are fixed in the direction of motion.

Figure 1 can be thought of as a snapshot where the vectors in this 2-D velocity field **V**(x,y) of *n*-dimensional space correspond to the optical motion of an object in the environment and possess both magnitude and direction. It is this pattern of vector directions that provide the ego motion information.

As an observer moves forward with his eyes and head held fixed, his retina receives an expanding motion

* The observer moves amongst static objects in the environment or all objects move together relative to the observer.

pattern emanating out from a singularity in the field - the focus of expansion. Gibson noted that this focus of expansion always corresponds to the observer's direction of motion or heading under conditions of pure observer translation (*figure 2a*). Movement perpendicular to his line of sight results in a uniform sheer across the field (*figure 2b*). Gaining heading information from this flow field would be trivial if the observer always kept his eyes and head fixed. However when observer rotations are added (*figure 2c*), e.g., when he moves his eyes or head to pursuit or fixate objects in the visual field, the focus of expansion no longer corresponds to the direction of heading, but is centered on the object of interest. This is the case because the flow fields produced by eye movements are purely propriospecific. In other words, these

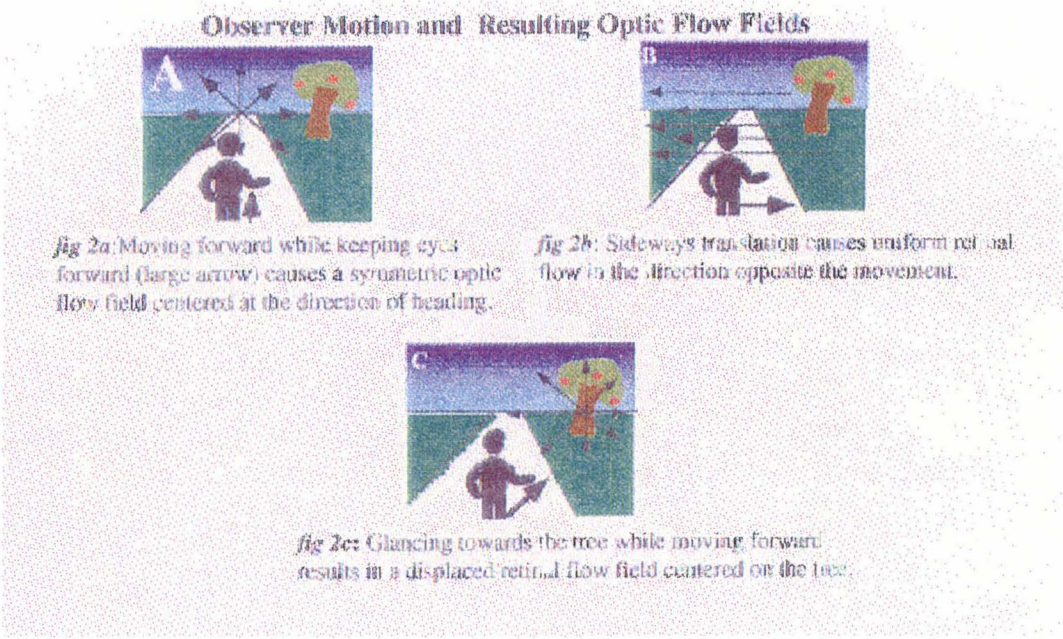


fig 2a: Moving forward while keeping eyes forward (large arrow) causes a symmetric optic flow field centered at the direction of heading.

fig 2b: Sideways translation causes uniform retinal flow in the direction opposite the movement.

fig 2c: Glancing towards the tree while moving forward results in a displaced retinal flow field centered on the tree.

[#] The formal convention is to define this array as the retinal flow, while the term optic flow is reserved for defining the spatial-temporal changes that arise in the optical array over time and is unaffected by eye or head rotations.

retinal flow fields are determined solely by the eye movement not by the structure of the environment the observer moves in.

The optic flow field is composed partly by the movement of the observer in the field *and* the structure of the environment. Chasles' theorem states that each movement of the observer can be thought of as being composed of both a translation and a rotation about an axis through a particular point in the world.[5] This rotation term is a rigid rotation of the optic array and therefore carries no exterospecific information. However, the addition of rotations in the velocity field is troublesome because in order to determine the direction of heading the visual system must be able decompose the rotational motion vectors of the eye from the flow field leaving the translation vectors.

Formal Analysis of the Optic Flow Field

We do know that in the cases where the eyes are held in the direction of self motion, heading can be computed from the translation vectors alone (as the magnitude of the rotation component is zero). Therefore, if we are to solve the problem of getting heading information from optic flow patterns, the flow field must be resolved into its two components. In other words, we must separate the translation and rotation contributions to the flow field. As the retina is the "screen" that all of the images project to, the eye is the most logical to start.

Longuet-Higgins and Prazdny, have formally described the motion of the eye and it's relationship to the optic flow patterns generated as the eye moves.[6] Following their lead, if the eye is taken to be a spherical projection surface *(figure 3a,b)* the

motion of the eye at any moment in time can be represented by the translational velocity of a point ***T*** on the eye relative to the world and the angular velocity of the eye about an axis ***OR***, where ***O*** represents a nodal point in the eye and ***R*** is some point on the surface.[7] If the observer is moving with his eyes and head held fixed the resulting translational flow field would be one where all of the other image points would lie along the "longitudinal" lines emanating from the point ***T***. If this sphere is rotating as well as translating, i.e. the eyes are pursuing, the image points on the surface of the sphere would have an additional velocity component representing the rotation of the sphere about the axis ***OR***. Therefore the optic flow field due to motion through a rigid environment is the vector sum of the translational field and the axial field due to the rotation of the eye about ***OR***. Again, we know that it is the translational component which corresponds to heading when the eyes are fixed in the direction of motion. Therefore, in order to obtain heading information the retinal flow field must be resolved in terms of its translational and rotational components.

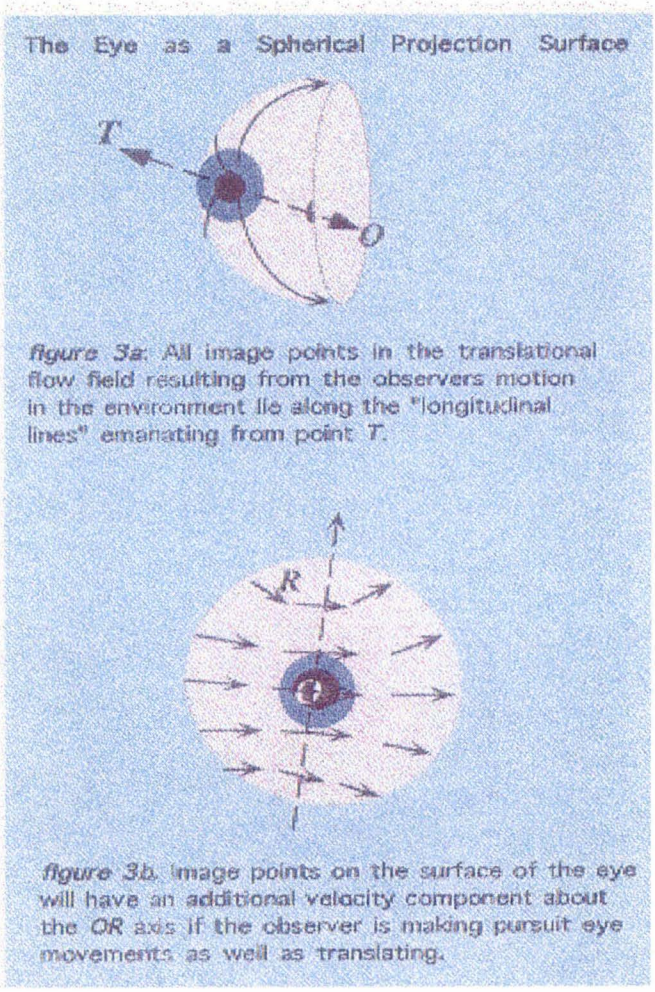


figure 3a: All image points in the translational flow field resulting from the observers motion in the environment lie along the "longitudinal lines" emanating from point *T*.

figure 3b. Image points on the surface of the eye will have an additional velocity component about the *OR* axis if the observer is making pursuit eye movements as well as translating.

In Longuet-Higgins and Prazdny's formal analysis of the flow field, the problem is restated in a Cartesian coordinate system ***OXYZ*** that is fixed with respect to the eye with retinal coordinates ***(x,y)*** for simplicity *(figure 4)*.[8] If the observer is situated at ***O,*** he is moving with translation (U_x, V_y, W_z) and rotation (A_x, B_y, C_z) with ***OZ*** representing his line of sight. The relative motion of a point ***P(X,Y,Z)*** is given by the following equations:

$$X = - U_x - B_y Z + C_z Y, \qquad \textit{eq. 2.1a}$$

and $$Z = - W_z - A_x Y + B_y X. \qquad \textit{eq. 2.2c}$$

Longuet-Higgins and Prazdny point out that, on the retina, the coordinates of ***P*** are given by

$$(x,y) = (X/Z,\ Y/Z); \qquad \textit{eq. 2.2}$$

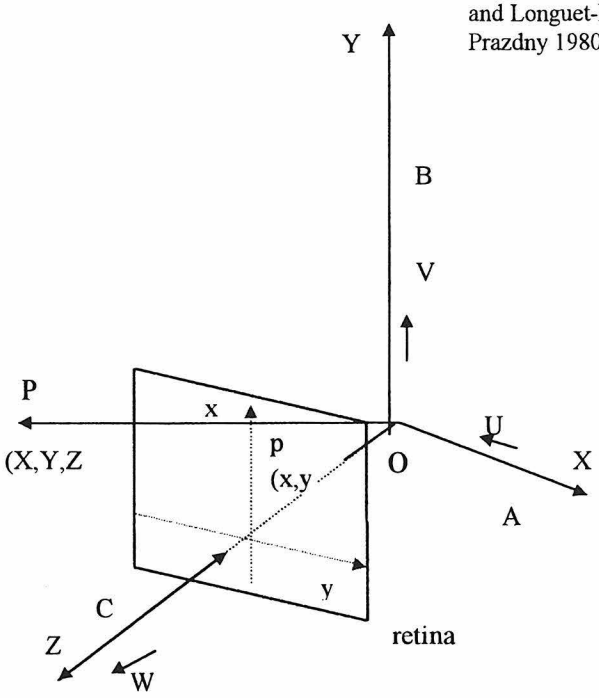
and its movement across the retina by

$$(u,v) = (x,y). \qquad \textit{eq. 2.3}$$

The optical velocity of ***P*** is arrived at by differentiating it's velocity with respect to time and then substituting in its position on the retina. In simplified form we get

Figure 4: Observer motion can be described in an external Cartesian coordinate system **OXYZ**. Here **OXYZ** moves with the eye while (**x**, y) represents the corresponding retinal coordinates (in red), **XYZ** represents the instantaneous position of some texture element P in the environment, **ABC** its angular velocity, **UVW** its translational velocity, **O** is the instantaneous position of the nodal point of the eye, **p** is the image of **P** on the retina, distance $\mathbf{OP_0}$ equals **R** (where **OR** is the axis about which the eye rotates), and **OZ** is his line of sight.

Adapted from Warren 1995 and Longuet-Hiigins and Prazdny 1980



$$u = u^T + u^R, \quad v = v^T + v^R. \qquad \textit{eq. 2.4}$$

Now the translational (u^T , v^T) and the rotational (u^R , v^R) terms are separate and independent of both the angular velocity of the coordinate frame and the 3-D structure of the scene. The translational terms do, however, depend on the distance **Z** from the observer. If we then write the translational component as

$$u^T = (x - x_0)\, W/Z\,, \quad v^T = (y-y_0)\, W/Z, \qquad \textit{eq. 2.5}$$

where

$$x_0 = U/W \text{ and } y_0 = V/W, \qquad \textit{eq. 2.6}$$

it follows that

$$v^T/u^T = (y - y_0) / (x - x_0). \qquad \textit{eq. 2.7}$$

The observer's heading can now be computed using the translational component vectors which are all directed away or towards some retinal point (x_0, y_0) where

$$U : V : W = x_0 : y_0 : 1. \qquad \textit{eq. 2.8}$$

[For a more complete analysis see Appendix A]

Computational Heading Estimation Models

Separating out the translation terms has solved the problem of obtaining heading information from optic flow patterns on the retina. However, our main question is only partially solved. In most viewing conditions, observers are constantly changing their direction of gaze as they move through their environment. For this reason we can not ignore the problem presented with the addition of eye movements. While the mathematical derivation above does a neat job of separating and thereby eliminating the rotation element, how does the brain perform this computation?

Just how do *we* separate our direction of gaze from our direction of heading? The brain is not privy to a priori knowledge of which vectors planar motions produce and which are due to radial motions. The brain only receives filtered information from the 2-D image on the retina. Many computational models have been proposed to answer this question. Most have been based on Gibson's early theories emphasizing optic flow. Although there are many varying methods, most approaches to the ego-motion problem fall into one of two categories. The first group - retinal image models, rely on the subtraction of the rotational component from the retinal flow to recover heading (pure observer translation)[9,10,11,12] or directly estimates the translational

component from the flow pattern and ignores the rotational component all together.[13,14,15,16,17,18] The second set - extra-retinal models, utilizes information about the eye velocity signal from extra-retinal sources such as efference copy signals from the oculomotor muscles driving the eye movement or proprioceptive signals from those same muscles. However different the methods of approach, all share the decomposition of the flow field into its translational and rotational components.

Retinal Image Models

The first group of models are called retinal image models. This approach exploits the differences between translational and rotational component properties. Translational flow is generally dependent on the depth **Z** from the observer as can be seen in the equations for translational flow (see also *figure 4*):

$$t_x = (xT_z + T_x)/ Z \qquad \textit{eq. 2.8a}$$

$$t_y = (yT_z + T_y)/ Z \qquad \textit{eq. 2.8b}$$

If t_x and t_y are set to zero, this results in the retinal coordinates of the observers' heading. However, when rotational components are present, the retinal image velocity information now has rotational components that, as can be seen in equations 2.9a and b, are not trivial to cancel out.

$$v_x = (xT_z + T_x) / Z - xyR_x + (1 + x^2) R_y + yR_z \qquad eq.\ 2.9a$$

$$v_y = (yT_z + T_y) / Z + xyR_y - (1 + y^2) R_y - xR_z \qquad eq.\ 2.9b$$

The following are short discussions of the various theoretical attempts to amend the complications caused by the addition of rotational components in the flow field.

Discrete and Least Squares Estimation Models

The first real attempts to understand the navigation from optic flow problem were essentially made in order to engineer robots and other automated machine vision systems that could utilize this information. These first models of heading measured the locations and displacements of a small number of points in the visual scene to set up a system of equations to recover the 3 translational and 3 rotational parameters that would uniquely describe the movement of an observer in the environment.[19202122] Discrete models needed only four to seven corresponding points in two successive motion frames to arrive at a direction of heading estimate. The same set of image features are followed from frame to frame. The sequence of their positions over time forms the input to a set of equations whose solution then leads to the parameters of motion and the three-dimensional structure of the environment.

While proving that it is mathematically possible to decompose the rotation component from the flow field, in order to arrive at a solution it requires very accurate displacement and position measurements. Any amount of noise in the visual field results in inaccuracies in heading judgments. Realistic environments are often filled with "noise". There are potentially conflicting visual inputs that arise from instant to instant

relative to an observer (e.g. navigating through a crowded market or swinging through trees) and yet humans and animals are able to navigate without incident. Therefore it is doubtful that this method is used by the brain.

Bruss and Horn utilized an iterative least squares method to search for possible surface features and observer movements that would be consistent with a specified optic flow pattern.[23] This approach does not rely on a continuos velocity field, instead it is optimized to yield a velocity field that best corresponds to observed image velocities. Based on the assumption that the apparent velocity of the brightness pattern in a scene varies smoothly everywhere in the image, the model compared information between the observed and the expected flow patterns from the entire field. Because of this global sampling method, these error minimization scheme are much less plagued by errors due to noise.[24,25, 26]

It is important to remember when discussing the relative strengths and weaknesses of these models, that the mechanisms presented above were designed not to give a biologically plausible method of extracting heading but as methods by which artificial systems can use optic flow to navigate. However they can offer insights as to what could possibly be taking place biologically. The error minimization/least squares models have led to neural network models that use the same principles. Notably Hatsopoulos and Warren's model incorporated the known properties of MT and MST neurons into their heading estimation network. Here they used templates that represent the flow fields produced by varying combinations of translations and rotations.[27]

John Perrone in a collaboration with Lee Stone, presented a model that also incorporated some neuro-physiological properties of neurons found in the middle temporal area of the macaque brain to analyze optical flow patterns. This two-tier scheme computes the direction and magnitude of eye rotations correspond to the retinal flow in the entire visual field. Heading direction is computed using translation detectors that are designed to discern the radial patterns that are generated by forward movements by observers. These translation detectors sum the outputs of direction and speed tuned motion sensors. The outputs of these sensors are not linearly related to the speed of image motion across the receptive field. Instead the models use these outputs directly, not estimates of image speed or direction. The motion sensors are arranged so that their preferred direction of motion lies along the radial direction out from the detector center. The detector with the most vigorous response signifies the heading direction.

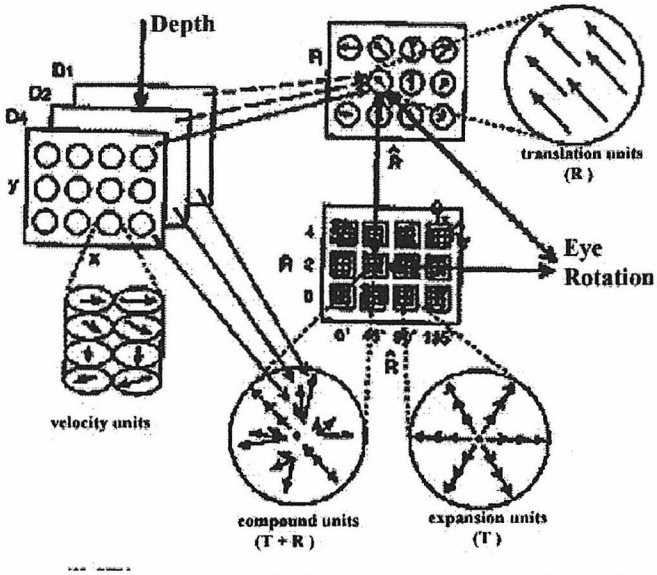


Figure 6: Template models decompose the translation and rotation vector components using MT and MST neurons as the biological framework. Here MT like units recover depth and velocity information. They then fed forward to MST-like units that are selective for various headings.

Differential Invariance and Differential Image Motion

The flow field has also been described as the unique combination of a translation, a rotation and a shear. In their 1980 paper, Longuet-Higgins and

Prazdny showed that the optic flow field can also contribute information about the slant and tilt of a surface at a particular point. The slant and tilt are found by taking the gradient of the retinal velocity vectors. Differentiating the retinal velocity vectors yields four spatial derivatives:

$$\mathbf{u_x}, \mathbf{u_y}, \mathbf{v_x}, \mathbf{v_y} \text{ - where u = x direction and v= y direction} \quad \text{eq 2.10}$$

representing the rate of change in the x and y directions. Combining these spatial derivatives can reveal interesting aspects of the optical flow field. First, if the u_x and v_y derivatives are added ($u_x + v_y$), this result tells us how much the image field is

Figure 5: The elementary flow components of (a)div, (b) curl, and (c) def and their corresponding higher order motion detection units. (Adapted from Koenderink, 1985)

expanding away from a point (its divergence or div). Subtracting u_y and v_x ($u_y - v_x$) gives the rate at which the image is rotating or swirling about the Z-axis (its vorticity or curl). The rate at which the field is simultaneously expanding in one direction as it

contracts in an orthogonal direction is found by combining $u_x - v_y$ and $u_y + v_x$ which is the deformation or def (*figure 5*).

Koenderink and Regan both suggested that a suitable heading detector could be made by a network of motion sensors each tuned to a particular direction of motion.[28,29] Differential invariant models are based on this interpretation of the flow field and essentially use the maximum divergence (div_{max}) to estimate heading. This seems logical because divergence, unlike curl, is not influenced by eye movements. Also, div is produced by translation toward a point unlike def which is produced by translation orthogonal to a point .

Koenderink and van Doorn further pointed out that the local minimum and maximum of the divergence are invariant under rotation. Therefore, they can be used to determine the direction of heading whether or not there were additional eye movements. One major problem with this approach is the maximum of divergence is not the same as the focus of expansion. The direction of div_{max} bisects the angle between the direction of heading and the normal to the surface. This rarely corresponds to the direction of heading. This problem exists because by using differential operators these models have incorporated information about the structure of the environment. This proves to be problematic because, while they are invariant with respect to the direction of gaze and eye movements, they are influenced by the layout of the environment. So although approximating the general direction of translation under conditions where there is low noise and robust flow patterns with smooth depth variations these models fail when flow information is sparse.

Other models were based on differential image motion and rely on motion or edge parallax. Motion parallax is the relative motion of environmental features that occupy nearby locations at different depths in the optic array which occurs at depth edges. Therefore these models require a three-dimensional environmental structure. Using Longuet-Higgens and Prazdny's interpretation of the problem, we have two objects at different depths along the direction of gaze, the object located closest to the observer has a greater two dimensional translational velocity, but their rotational velocities are the same. As we saw in their formal analysis of the flow field, the translational component of flow depends on distance while the rotational component does not. These vectors radiate out from the heading point. When there are no head or eye rotations they point along the direction of heading.[30] When a rotational component is introduced to the flow, the vectors from these objects no longer point in the heading direction. If we subtract these two vectors from one another, the direction of heading will fall somewhere along the resulting vector. If two subtraction vectors are created in separate spatial locations in the scene their intersection point marks the heading.

These models can successfully distinguish between the direction of heading and the direction of gaze. However they fail when confronted with environments without depth variation (i.e. again the frontal plane). Another problem with these algorithms is that they also only recover the translation axis and not the direction of translation. This can be remedied if information about the relative depth of objects in the flow field is provided.

Rieger and Lawton took a similar approach[31] expanding the Longuet-Higgins and Prazdny model to include relative motion between nonoverlapping elements within a segment of the visual scene. By taking the difference vector to be the relative motion between two nearby elements in the scene, they produced vectors radiating out from the heading point. This model also has draw backs in that it requires some depth variation within each segment to produce differential motion that are discernible. This means that it would also fail in the case of approach to fronto-parrallel plane.

Dynamic and Flow Asymmetry Models

In 1989 Verri, Girosi, and Torre proposed a scheme where they described the flow field as the phase portrait of a dynamical system. Based on theories of planar dynamic systems, the movement of an observer is determined from the local structure of flow in a region of singular points in the visual field over time.[32] In order for the model to yield useful results, there needed to be dense flow about the singular points. In other words, there can not be any field discontinuities and the flow field itself must be robust. The parameters used are structurally stable and thereby are not as susceptible to noise in the flow field. While noise may not be a problem, the dynamic model still relies on a smoothness constraint.

A simpler approach is to provide the observer with asymmetries in the flow field.[33] [34] It is proposed that the pattern of these asymmetries can lead the observer to the singularity in the field. In this case the heading point would be surrounded by a symmetrical flow pattern. Asymmetrical models are also heavily dependent on the

structure of the environment. For the model to arrive at a correct heading judgment, it must be provided with robust flow about the singular points in the field and, like the dynamic model, assumes field smoothness.

Although supplying users with a good approximation of heading, retinal image models fail under many conditions that are potentially behaviorally relevant. Because they rely solely on the information on the retina, the models require depth information and variations in the scene. In addition, these paradigms also fail if the rotational flow components are significantly larger than the translational ones and if the field of view is small. Extra-retinal models attempt to get around these problems by having the additional property of utilizing eye movement information.

Extra -Retinal Models

So far we've reviewed models that rely solely on the information provided by the retinal flow patterns. Extra-retinal models also employ information about the eye velocity signal from extra-retinal sources such as efference copy signals from the oculomotor muscles driving the eye movement or proprioceptive signals from those same muscles.[3536] This approach has many advantages over retinal image models. Not only do they offer independence from the scene geometry and field of view, they also offer this heading estimation in head centered coordinates.

These models also have drawbacks. In cases of reduced field cues, the visual system underestimates pursuit eye speed which causes biases in heading judgments that

are inversely proportional to the eye speed.[37] Since both methods have disadvantages in real world conditions, the visual system may use both retinal and extra-retinal input to recover heading from optic flow

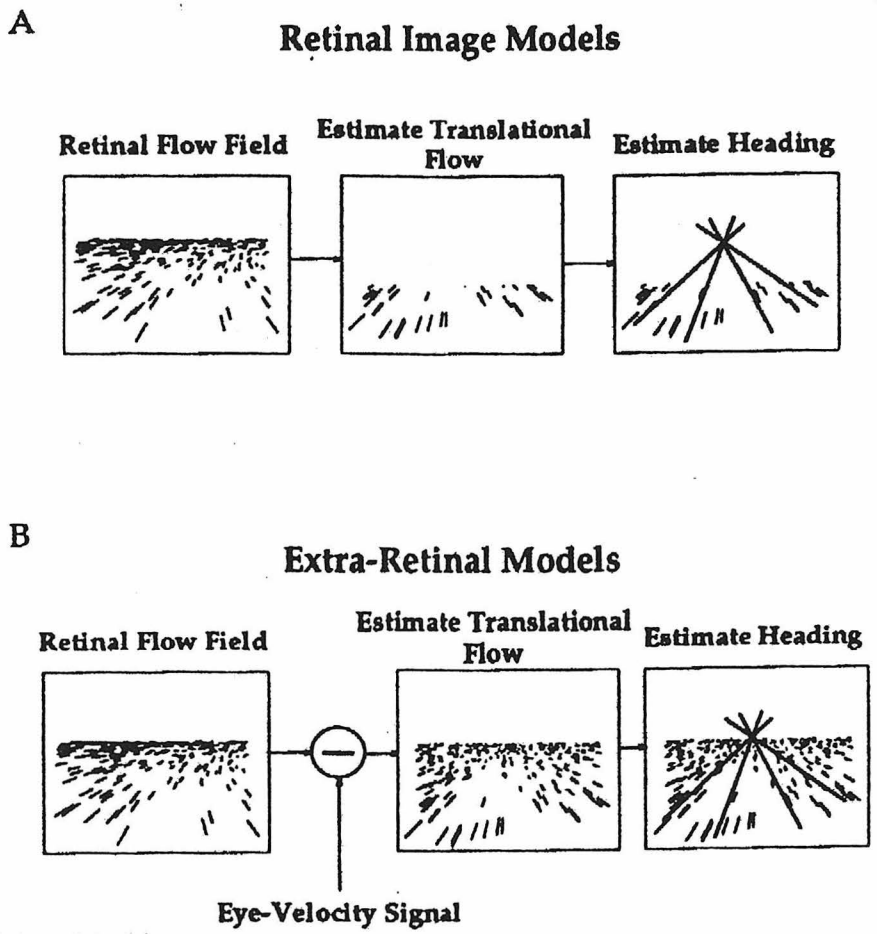


Figure 7: Retinal image models take the raw image vectors from the flow field (panel A-1) eliminate the rotation vectors(panel A-2) and then estimate heading from the estimated translation vectors. Extra-retinal models take the raw image (panel B-1), then take into account information about the eye movement to take a more robust estimate of the translational component of the flow field (panel B-2) from which to make an estimate of heading (panel B-3). (from Royden et. al, 1994)

information. It has been argued that Gibson's early insight that optic flow was an important tool in determining heading has resulted in many models determined to

recover heading from the optic flow field when the information needed is readily available in the retinal flow.[38] Regardless of which side of the debate proves to be true, there has been many new insights gained from these computational models that have lead to a more concrete understanding of the problem of navigation. These models set the stage for the parameters that needed to be considered such as flow field noise, depth variations in the flow field, and the number of elements in the flow field, when designing human perception experiments. The following chapter will discuss human perceptions of self-motion more particularly if humans can indeed determine their direction of heading from optic flow fields.

CHAPTER 3:
Human Visual Perceptions of Heading



Although we are not on the rollercoaster, we get a sense of motion due to the configuration of the tracks. The rails appear to be emanating from a common point in the dip . In a more formal setting can we fool our brain into thinking that we are moving and if so how do these simulations fair when we actively pursue objects in our visual field?

3

Self navigation or ego-motion is something we seldom , if ever, think about, although it is vital to our everyday existence. Whether we are walking down the street, driving in our cars, or, as the picture at right indicates, riding on a roller coaster- in order to navigate successfully we unconsciously but accurately determine our direction of heading. As we are sitting in the moving trolley with our eyes fixated expectantly on the opening ahead of us, our gaze is, for all practical purposes, stationary and our retinas receive an expanding motion pattern radiating outward from our direction of heading- the dip in the track that lies ahead. The visual patterns on the retina that arise from our movement in this environment are what are commonly referred to as optic flow fields.

Ego-motion Perception from Optic Flow

In 1950, James Gibson first proposed that the structure of the optic flow field provides valuable ego motion information for observers.[3940] An example of the power of optic flow stimuli on our perception of motion can be seen in our experiences at the cinema. We have all been to the movies and have been forced through clever camera manipulations to see the world from the vantage point of the actor. In that situation although we are sitting firmly in our seats, we get the strong sensation of movement. Long before motion pictures became possible, showmen were using the same optic flow principles to create sideshow illusions in circuses (namely the haunted swing illusion).[41] These situations generate perceptions that are similar to those we experience in the real world because in both cases the motion patterns of objects in the visual field on the retina are the same.

Retinal image motion can be generated by either the movement of the observer or of objects in the environment. Here we will consider the movement an observer, a pilot, relative to a stationary environment, a cloudless sky (*figure 2)*. When the pilot looks straight ahead, *figure 2a*, her line of sight is defined by the vector originating at her nose and ending at the point she fixates on the horizon, ***p***. If she moves forward perpendicular to her line of sight a translation motion occurs. The radial motion produced on the retina from this translation will be either expansive, if she moves forward, or compressive if she backs away. In most instances of forward motion, the retinal image patterns seem to all originate at a common point in the visual field - the focus of expansion (FOE) which also corresponds to her heading. If she rotates about

the line of sight (*figure 2b*), this produces planar rotation motion. These translational, radial, and planar motions can be described by the mathematical functions the first

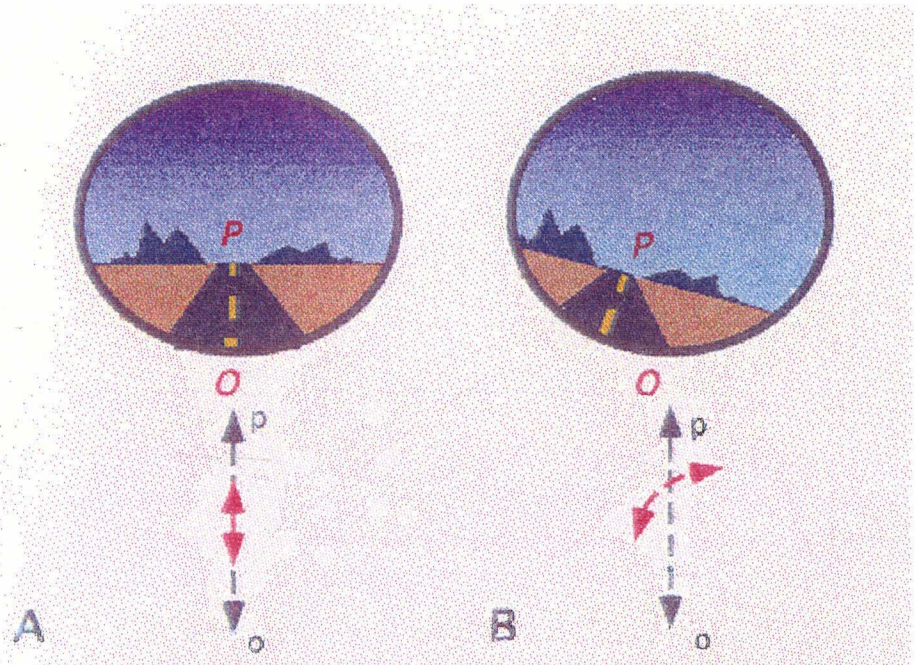


Figure 2a. When moving parallel to the line of sight, OP, (dashed black double arrowed line), either expansive or compressive radial motion (red double arrowed line) occurs.
Figure 2b: If instead the pilot banks the plane about the line of sight, the retina receives rotary motion.

derivative, the divergence (div), and the curl.[42] Gibson's postulation was that we use this information to determine, among other things, our direction of heading.

Those figures illustrated the flow fields that occur when the observer's path was straight and she travels with her eyes fixed in her head. Here the problem of navigation is a trivial one because her direction of heading is always the focus of the expansion field. In the real world we are free to move our heads and eyes to look at objects in our visual field. Take this sign for instance(*figure 3*). If we direct our gaze from the road in order to look at the sign , the image on our retina also shifts. Now the

stimulus pattern originates from the sign which is now our center of gaze and not the mountain which is our true destination point. We know from personal experience that when we make similar eye movements that we are not heading into the object of our attention. If Gibson's hypothesis that we determine our heading using optic flow is correct, humans should be able to accurately perceive their direction of locomotion from optic flow patterns with and without eye movements.

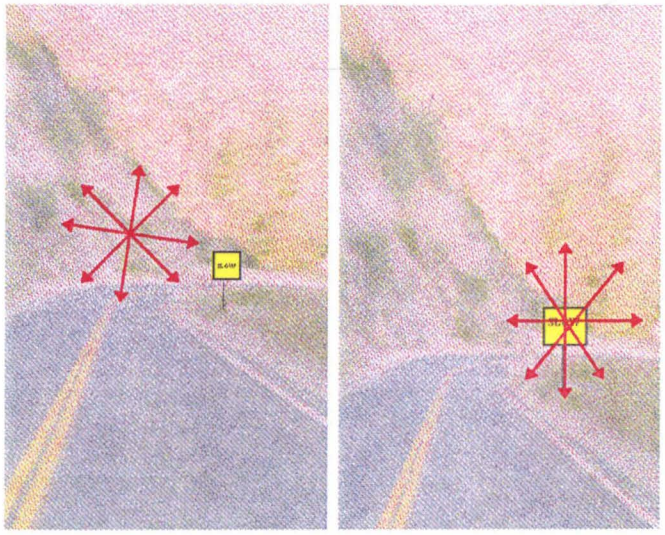


Figure 3a: As we go down the road, our heading corresponds with the focus of expansion.

3b: If we shift our gaze to read the sign this is no longer true. Our heading and the FOE are

Translation

Psychophysicists have simulated the optical flow fields arising from observer movements on computer generated displays. Studies conducted in the 1970's concluded that subjects are quite poor at determining direction of heading based on optical flow alone, with our without eye rotation.[43] [44] In their 1988 study Warren,

Morris, and Kalish allowed observers to view moving random dot displays of infinite lifetimes and asked them to discern whether they were moving to the left or the right of a probe that appeared at the end of the trial. In this series of experiments, they simulated observer movements along ground planes, fronto-parallel planes, and through 3-D clouds of dots. In doing so they found that humans can indeed determine their direction of heading using only optic flow with an approximate accuracy of 1-2° and a 75%- correct threshold. These results were in line with Cuttings' earlier estimation that heading accuracy needed to be between 1 -3° in order for observers to perform behavioral tasks such as obstacle avoidance.[45]

Human perceptions of heading remained intact even at slow simulation translation speeds, consistent with the optic flow experienced when walking, and if the display time was reduced to 280ms. If the dot life times were also reduced to two frames per 3ms display, subjects still retained their ability to make good estimations. In other experiments that asked subjects to make judgments about their future course on a circular path or as they "traveled" through a 3-D cloud of dots similar results were obtained(49, 264). Here high performance was maintained with thresholds below 2 degrees.[46,47] Among other things, these results indicate that the instantaneous velocity field is adequate for estimating heading under conditions of pure translation.

In order to determine just what aspects of the flow filed provides the effective information for heading, Warren et al., added speed and direction noise to the individual dot motions. This was achieved by randomizing the magnitudes of individual dot displacements while preserving their direction. In cases of both translational and

curvilinear motion when the global orientation of the velocity vectors was kept intact, but the lengths of these vectors were randomized (creating a "direction" field), heading judgments remained accurate. If instead the directions of the vectors were randomized while conserving their speed (creating a "speed" field) there was a marked decline in performance. Apparently then the radial pattern of vector directions is invariant with respect to the 3-D environmental layout and not vector speed. Vector speed is greatly influenced by the 3-D structure of the environment. In other words the radial pattern of vector direction and not their vector magnitudes is what allows for adequate heading judgments.

A few insights can be drawn from these experiments. The first deals with the structure of the viewed environment. Since there is consistent behavior across viewing conditions there is support for Gibson's notion that the visual system does not assume surface smoothness. Also when the number of dots was increased performance increased.[48,49,50] So rather than locating a singularity on the field, the visual system may be exploiting the redundancies in the radial flow pattern.

Second, the results of the altered speed and direction field experiments show that perturbing the speed field does not affect heading estimations if this perturbation is done in a random fashion. However, the Dyre and Andersen study found that if there are pockets of perturbations (say on one side of the focus of expansion) the observer has the feeling of moving on a curved path.[51]

Translation and Rotation

The results from the translation experiments prove that humans can readily identify their heading direction when moving through a rigid environment employing only optic flow information. The question now is what happens when these radial patterns are confounded with the rotations added by eye movements. It has been argued that the brain could utilize information from a variety of other sensory modalities, namely the vestibular, oculomotor, and/or motor systems. However, given that strong perceptions of ego-motion can be generated from passive viewing simulations of motion, the visual system alone must be able to provide the necessary information for judging heading.

In the last chapter we reviewed many decomposition models that proposed solutions for this problem. These many solutions can be placed into five major categories: 1. *Discrete* models needed only four to seven corresponding points in two successive motion frames to arrive at a direction of heading estimate, but these failed due to their need for very accurate displacement and position measurements[52]; 2. *Differential invariant* models used the local maximum of divergence (div_{max}) to estimate heading, however this rarely corresponds to the direction of heading[53]; 3. *Differential image motion* models rely on motion or edge parallax. These models require a three-dimensional environmental structure; 4. *Flow pattern asymmetries* have also been proposed. These require the subject to perform multiple fixations; 5. *Extra-retinal oculomotor motor signals* could also compensate for eye movements by way of an efferent copy.

The results from the modeling offer some insights as to the relevant parameters psychophysicists should consider. Most models sited noise in the flow field as a primary deterrent to their heading estimation ability (~10% maximum tolerated).[54] Others were constrained by the availability and independence of depth information.[55, 56] Some needed a requisite number of elements in the flow field each with a specified lifetime.[57,58,59] Other requirements included a continuous flow filed, low rotation to translation ratios, lower limits on the size and duration of the visual scene.

The first psychophysical attempt to determine whether humans could accurately perceive their heading with or without extra-retinal information used simulated eye rotations to compare with real eye movements.[60] In their 1985 study, Reiger and Toet had observers view a scene simulating their translation toward one of four points on, and rotation about a randomly selected axis on one or two transparent fronto-parallel planes. The first plane was situated at 3m while the second was at 12m from the observer. The rotation rates varied from 0 to 1.8 °/sec. Here they found that observers could *not* determine their correct heading with higher rotations with one plane but *could* do so with a simulated approach to two planes. While this result suggests that some depth information is needed it would seem that extra-retinal signals are not necessary.

Warren and Hannon also designed a perceptual experiment to determine if humans could derive heading while making simultaneous eye rotations. In a preliminary set of experiments, they compared heading judgments during stationary fixations and smooth pursuit eye motions. This experiment tested the need for edge parallax cues

and multiple fixations. In one half of the experiment, they presented ground plane translations with a stationary fixation point. After the display, subjects were asked to judge whether they were translating to the left or right of a vertical bar at the horizon. In the other half subjects were asked to track a moving fixation point on the ground plane. This pursuit eye movement added a rotational component to the translation. The two conditions were interleaved randomly. If observers require edge parallax or multiple fixations in order to make valid estimations, you would expect that their performance in the moving eye condition would be at chance. They found that observers could judge their heading with an accuracy of 1.7° when fixating a stationary point and 1.8° when the fixation point moved, without edge parallax cues available in the scene or multiple fixations. This result rules out the differential image motion, flow field asymmetry, and ocular drift models as valid biological solutions to the problem.

Performance in conditions with simulated approaches on a ground plane and through a 3-D cloud of dots were comparable (1.7°/1.8° and / respectively) . This was true even when subjects tracked a feature (through smooth pursuit eye movements) that was away from the direction of heading. However, if the rotational component to the retinal flow was added directly to the visual stimulus on the screen, simulating the effects of eye rotation, performance dropped for the approach to a vertical plane, but remained high for the two other conditions. Note that in both the actual and simulated eye rotation sets of conditions, retinal flow is identical. Any performance change had to be a consequence of extra-retinal information about eye movement. Warren concluded that subjects could determine direction of heading from

optical flow alone, with or without eye rotation, as long as depth variation was present in the stimulus.

Experiments by van den Berg also confirmed Warren and Hannon's conclusions.[61,62,63] Here, van den Berg had observers view random dots on a ground plane. Some of the dots were "signal dots" and others were "noise dots". The noise dots moved in a random fashion not relevant to the simulated direction of movement while signal dots were. He found that subjects were equally adept at determining their direction of heading whether there were real or simulated eye movements when there were more signal dots. If, however, more noise was created by increasing the amount of the randomly moving dots, observers retained their accurate judgments when really moving their eyes but had trouble making correct estimates if they were presented with simulated eye movements. Therefore, human perceptions of heading are more robust when presented with a high signal to noise ratio, when real as opposed to simulated eye movements are made. This also corresponds nicely with the predictions made by the retinal image models.

The problem with the above mentioned experiments is that the pursuit speeds used were very slow (0.2 to 0.7°/sec in the Warren and Hannon experiment and <3.2°/sec in the van den Berg studies). While these speeds correspond to typical pursuits generated while observers are walking, they leave out a wide range of possible speeds that occur when observers track objects while they move more quickly, while running or driving. It has been demonstrated that extra-retinal models perform poorly when pursuit speeds are this low.[64 65] This fact alone makes the Warren and Hannon

result that subjects do not require an extra-retinal signal less compelling. In order to determine whether extra-retinal signals play a significant role in heading estimation a wider range of pursuit speeds must be examined.

In 1992 Royden, Crowell, and Banks tested observers' abilities to judge heading while making pursuit eye movements at moderate speeds and under conditions of simulated pursuit eye movements. Observers viewed a random dot display simulating approach to two transparent fronto-parallel planes for 800 msec. The simulated observer translations were 100cm/sec and the direction was between -5 and 5° from the center of the screen. The rotation speeds tested were 0, 1.25, 2.5, 5, and 10°/sec and were presented in two sets of five interleaved staircases. A 2AFC procedure was used to estimate the heading discrimination thresholds. They found that subjects made fairly accurate judgments of heading under real eye movement conditions. Their findings under simulated conditions confirmed many of Warren's findings for slower rotation speeds (in fact the average threshold at 0.62 °/sec was the same for both groups at 1.4°). However, Royden et al found increased discrimination threshold with increased rotation rates. They then concluded that observer estimates of heading were less accurate at rotation rates that were greater than 1.25°/sec when the eye movements were simulated. This could mean that extra-retinal eye movement signals are important for determining heading when observers are moving at speeds greater than those experienced while walking and tracking objects away from the heading point.

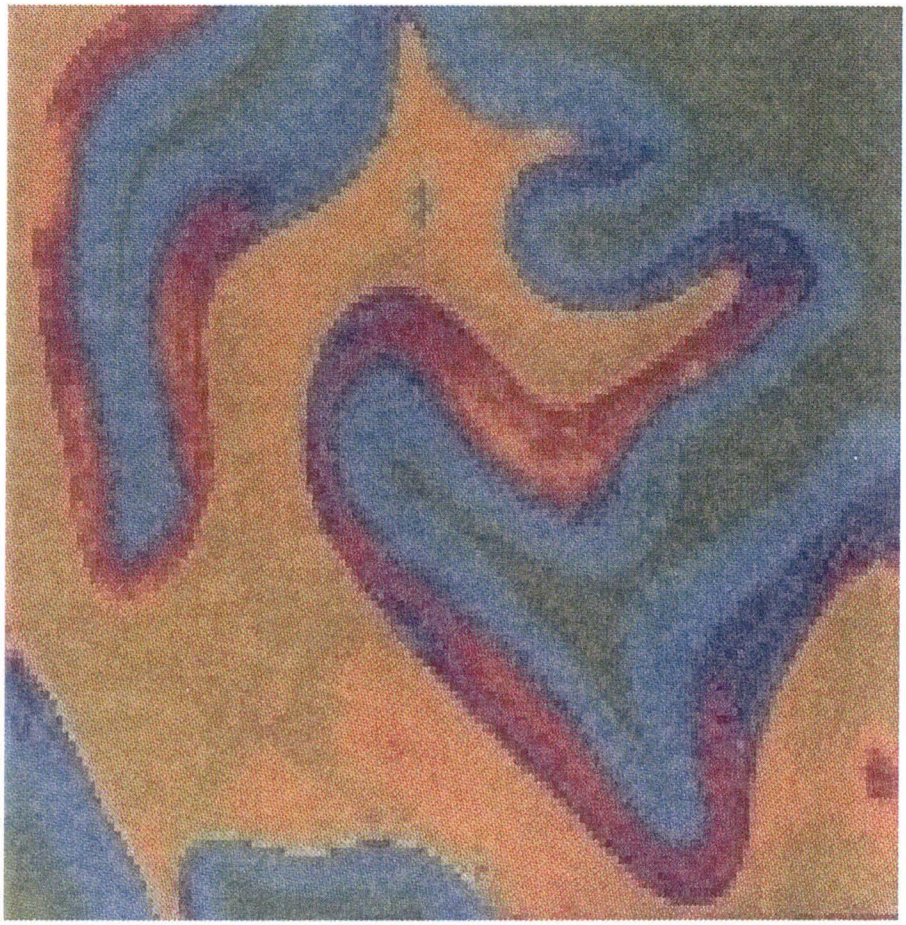
At first glance Royden et al's results may seem to contradict those of Warren and Hannon and van den Berg et al. However, the important difference between the former group and the others was that the viewing environment was not a ground plane. Both Warren and van den Berg simulated observer translations parallel to a ground plane while fixating points on the surface creating a horizon cue. If this cue is eliminated (van den Berg 1993- experiment 6) subjects can no longer make estimates of heading. This indicates that the horizon can be another possibly relevant cue that observers use in order to determine their heading.

Human perceptions of heading under optimal conditions can be carried out accurately based solely on optical flow. However extra-retinal signal are required as conditions deteriorate due to lack of depth variations in the stimulus, noisy conditions, or under high rotational eye velocities. A somewhat analogous situation exists within the psychophysical literature with regards to localizing visual targets in space. When the extra-ocular muscles of the observer are partially paralyzed, subjects had a hard time identifying target location in the dark, but had no trouble in the light.[66] These results suggest that retinal and extra-retinal mechanisms may work together in the primate visual system to enable observers to accurately estimate their heading in natural environments.

It has established that humans can use optic flow information to determine their heading whether they are making purely translational movements in the environment or if they execute eye rotations as they translate. This is done with relatively high degree of accuracy in both conditions and without much difficulty. It is now a question of

where in the primate brain this ability to extract ego motion information from the 2-D projections of light lies. The next chapter will review the literature about a possible candidate in the extrastriate visual processing stream- area MSTd.

Chapter 4:
MSTd: Anatomy, Physiology and Function



This colorful slice of macaque brain includes areas LIP, MT, and MSTd. There has been much speculation that MSTd is the area that could support heading estimation. What are it's attributes that lead to this conclusion?

4

Although humans are capable of making accurate judgments of heading from optic flow stimuli in a variety of visual environments it is not clear what neural areas make this possible. From the results of both the computational models and the human psychophysics experiments we have a basis from which to look for the neural mechanisms that enable heading. There are two main requirements of this area: 1. In order to compute heading, the brain, like the computational models must be capable of processing higher order complex motion stimuli; and 2. This area should also have some connections with areas that receive oculomotor signals. While there are many motion sensitive areas in the primate brain that possess one of these qualities, one area that meets both requirements is area MSTd.

ANATOMY

Lying deep along the anterior bank of the superior temporal sulcus (STS) is MST- the medial superior temporal area (*figure 1*). MST sits on a long 4 - 5mm strip of cortex mediolateral to area MT.[67,68] A member of the extrastriate visual processing stream, MST gets its inputs from prestriate visual cortex, has intermediate connections with parietal areas, and projects forward to frontal eye fields and areas in the rostral STS. The main

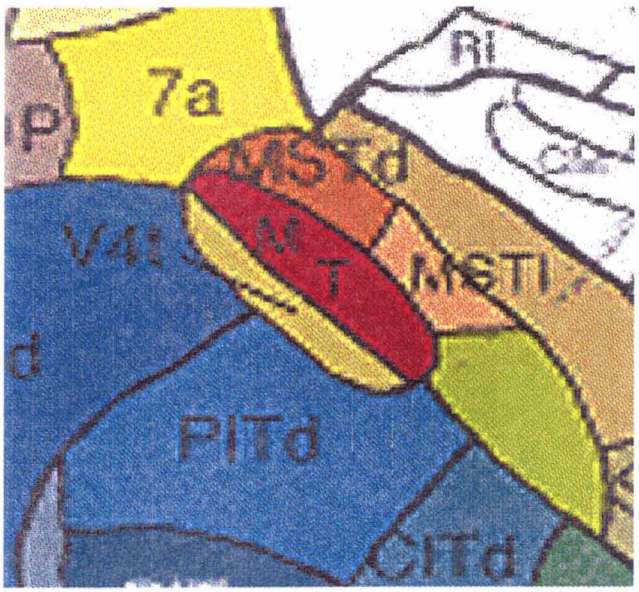


Figure 1: In this map of the macaque brain, the superior temporal sulcus has been opened and flattened. MST is shown in orange (MSTd) and peach (MSTl) adjacent to the middle temporal area (MT-red) and area 7a (yellow). *From Felleman and van Essen.*

reciprocal connections are to the medial subdivision of the pulvinar and the claustrum with non-reciprocal connections to the striatum(caudate and putamen), the reticular nucleus of the thalamus, the pontine nuclei and the nucleous of the optic tract.[69] Within the STS, MST is reciprocally connected to the polysensory association areas which are thought to mediate the convergence of information from several sensory modalities.[70] MST also has a decending contact with the lateral terminal nucleus of the accessory optical system which is known to allow for the processing of self-motion in birds and rabbits.[71, 72] Other projections from MST include those to areas LIP and VIP (the lateral and ventral interparietal areas) in posterior parietal cortex, areas thought to be involved in the representation of external space, and the frontal eye fields.[73 ,74] Finally, MST also has strong lateral connections to FST and receives most of its input from area MT- an area containing a high proportion of directionally selective neurons (*figure2*) .[75,76,77]

PHYSIOLOGY

MSTd is a midlevel area in the magnocellular pathway responsible for processing visual motion information. At first, MST was thought to be a functionally uniform area, now it is divided into three subregions: the dorsal (MSTd), ventro-lateral (MSTl)- both representing the central visual field, and an intermediate area (MSTi) region which represents the

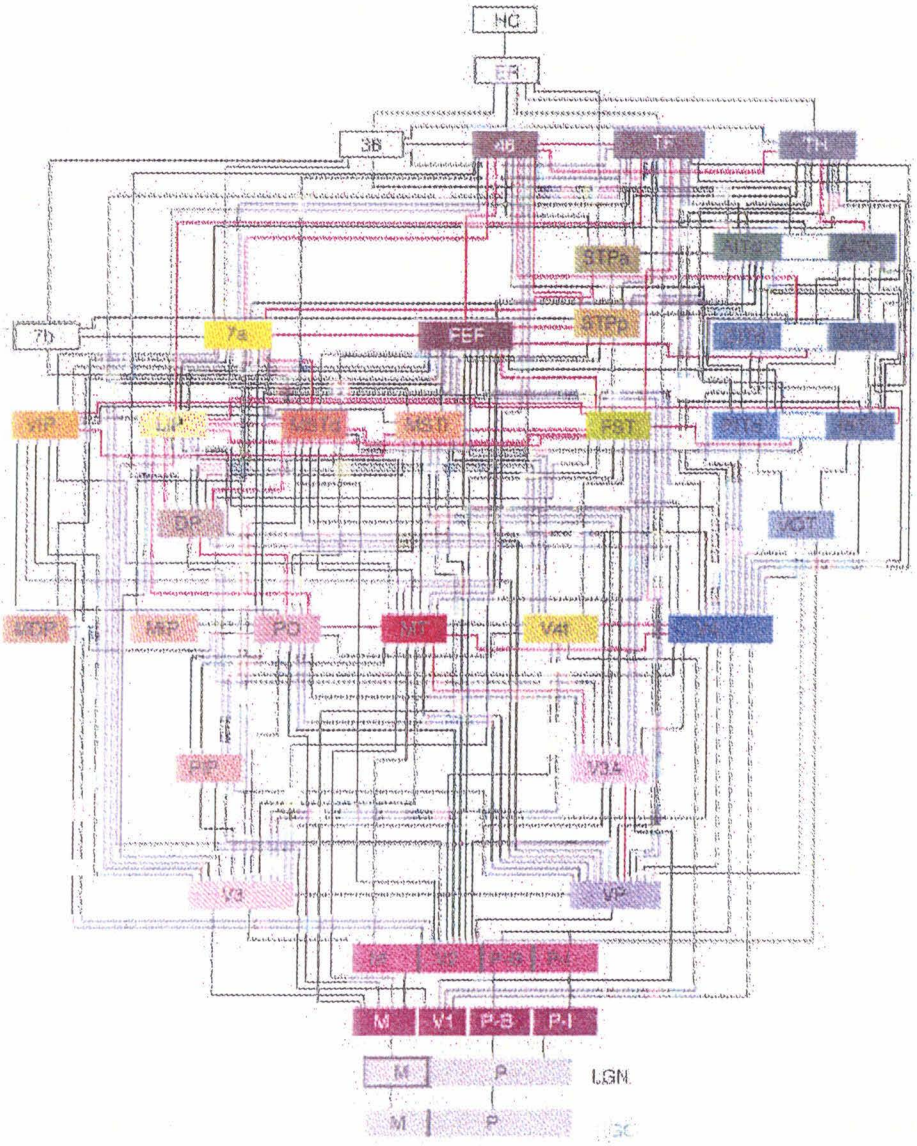


Figure 2: This diagram of connectivity in macaque visual cortex from Felleman and van Essen shows MST (represented by MSTd and MSTl again orage and peach) and its heavily interconnections with, among other areas, MT-red, forward connections to the frontal eye fields (FEF-brown), and area 7a -yellow. MST also shares lateral projections with FST-lime green, the lateral interparietal area (LIP- corn), and the vental interparietal area (VIP-mustard). *From Felleman and van Essen.*

periphery.[78,79,80] While it is still debated whether or not MSTi is actually represents a disticnt cortical area, MSTl and MSTd are thought to be. With respect to motion analysis, MST neurons have been divided into two classes, those that recognize figure motion and those selective for field motion analysis. These figure/field distinctions are clustered with respect to MSTl and MSTd. MSTl contains a higher proportion of figure selective cells. These neurons respond favourably to the translational motion of individual features in their receptive field. The field selective neurons are localized in MSTd and are characterized by their preference for movements of large fields of these stimulus features. [81,82,83]

In the field selective cases, the MSTd neurons often reverse their motion direction preference if the size of the stimulus changes. This phenomena can be linked to MSTd's disparity tuning. Much like the neurons found in MT, MSTd cells are disparity tuned. However, unlike MT which is tuned for either near or far , MSTd neurons are broadly disparity tuned coding for both near and far disparity.[84,85] A majority of these neurons (~60%) modulate their responses to linear motion depending on the depth at which the movement was initiated while keeping their response to the direction of movement constant across disparities. The remaining neurons (~40%) reversed their direction preferences once the target moved to another disparity.[86]

MST neurons also have interesting physiological responses when presented with smooth pursuit stimuli. In an experiment conducted by Newsome et al in 1988, the macaques' ability to smooth pursue a target was impaired when a lesion including MST was made. The object of the task was for the animal to make a visual saccade to a target and pursue if it was moving or fixate it if stationary. In this experiment saccades to stationay targets were unimpaired. This deficit was explained as being caused by the animals inability to recognize the motion of the target. If no motion is detected then no pursuit mechanism is initiated. The maintenance of pursuit was also adversely affected following MT/MST lesioning. Here the animal could not maintain fixation either.[87] MSTd and MSTl cells may serve different roles in the smooth pursuit network. MSTl neurons are thought to code for the retinal slip of the target. These neurons may feed the signals to motor areas that make the adequate adjustments so that the pursuit can continue. MSTd neurons, on the other hand may play a more supporting role. These cells seem to be activated by an efferent copy of the motor signal used to drive the pursuit.[88,89,90]

MSTd AND OPTIC FLOW

While these and the previously mentioned physiological properties of MST neurons are fascinating, it is the selectivity for expanding, rotating, and spiraling flow patterns in MSTd that has sparked the most interest. Of the two functional subregions, MSTd is by far the most carefully studied. As mentioned

before, neurons in this area not only prefer large motion stimuli, they are broadly speed tuned (low 1 degree/second and high 20 degrees/second) and most are directionally tuned with respect to translational motion. [91,92,93,94,95]

In a series of studies conducted in the 1980's Hide-Aki Saito's laboratory conducted studies of MST and found that there were three unique types of visually responsive neurons in this area. The first population of cells were receptive to straight frontoparallel movement in a particular direction, the second group for expansion/contraction, while the third responded to clockwise/clockwise rotations. While directionally selective cells were found throughout MST, only the dorsal portion contained neurons that responded to expansion/contraction or rotations. In all cases, the neurons preferred movements occurring over a wide field. They also found that the neurons selectivity for expansion/contraction and rotation patterns on a wide textured field depended on three stimulus factors: 1. the direction of regional movements, 2. the speed gradient of regional movements, and 3. size changes (expansion/contraction) and inward acceleration (rotations) of stimulus features. Of all three factors, it was determined that the limiting factor for the activation of MSTd neurons was the spatial arrangement of the stimulus features (radial arrangement- expansion/contraction; circular arrangement-rotations).[96]

This global pattern selectivity is used to characterize MSTd neurons and can be for linear motion, divergence, curl, and deformation. All neurons in MSTd respond to translational motion and all EFC's have some element of translation in them (figure 3a).

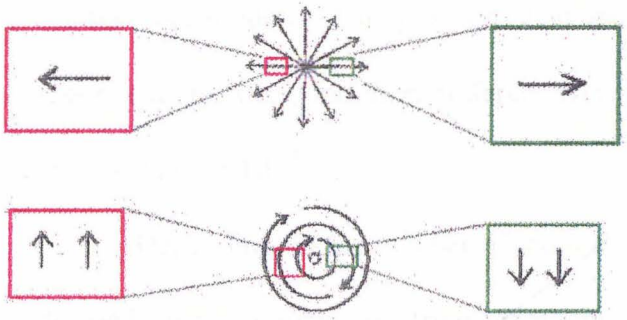


Figure 3: A)If an expanding stimulus is viewed through the red aperture the motion appears to be linear and to the left. However, if the aperture is shifted (now green) the motion appears to be to the right. B)Rotating patterns have a similar effect. However the motions are now upwards(red aperture) or downwards(green aperture) when the pattern rotates in a clockwise fashion.

Therefore in order to determine a cell's selectivity for a particular global motion pattern, this preference must be proved to be independent of it's selectivity for any translation evident in the stimuli. If an expanding stimulus is viewed through an aperture (figure 3b), it appears to be a translation, in this case rightward. Based on this alone, this neuron could be a directional cell, firing because rightward motion is in its receptive field. If this cell is truly tuned for direction and not a particular elementary flow component (EFC), then moving the pattern to another position within it's receptive field would cause the neuron to change it's preference from this expansion to contraction in order to

preserve the selectivity (figure 3c). If the global motion pattern is moved to a new location in the receptive field and the neuron retains its selectivity then it can be said that this neuron is tuned for the global motion pattern and not just translational motion. This position invariance with respect to flow type (also speed, cue, features, and form preferences) is so robust that it is used to identify presence in MSTd.[97]

Depending on the number of motion types they respond to, neurons are deemed single, double, or triple component. There seems to be an even distribution of these cell types in MSTd.[98,99] Single component neurons respond to expansion, contraction, a rotation, or a translation. These cells are the most directionally selective, are highly positionally invariant with respect to stimulus placement in their receptive fields, have significant inhibitory responses, and tend to have overlapping excitatory and inhibitory subregions.

While classification of the single component cells have been straight forward, the characteristics of the double component cells are not yet universally agreed upon. One mode of classification has double component (DC) neurons responding to all elementary flow components in combination and with translation.[100] Another has DC cells responding for EFCs in combination with translation but not in combination with other EFCs (say spirals formed with expansions and rotations).[101] While yet a third group found EFC responses but no evidence of selectivity for an EFC in combination with translation.[102] Finally, the triple component neurons act on a whole opposite to

the single component cells. They are the least directionally selective, exhibit the lowest position invariance, are not very inhibited by antipreferred stimuli, and are the least likely to have overlapping excitatory and inhibitory subregions.[103]

The discrepancies in determining what stimulus drives a cell may have resulted from the differences in experimental procedures used to generate the patterns. The first studies of MSTd neuron selectivity used hand held stimuli or a slide projector with a zoom lens that projected a random dot pattern on the viewing screen.[104] There are several problems with this method of presentation. First, the apparent size of the dots varied as they were zoomed in to represent expansion and out for contraction. Second, when the dots were rotated a curved trajectory was produced while that for the expansion and contraction was linear albeit with an added speed gradient (the dots appeared to accelerate or decelerate when zoomed in or out respectively). While none of these cues could independently elicit a response (with the exception of the speed gradient, which did elicit a slight response,) from a MSTd neuron, ideally all the stimulus patterns should be directly compared. Later studies used computer-generated displays that controlled for these artifacts.[105]

Another possible explanation for the disagreement could be that the stimuli used to determine the neuron's preference wasn't optimal. While the single component cells are not in question, the double and triple component cells may actually prefer neither expansion nor rotation but a particular combination of the two. This would explain the seemingly multicomponent

nature of the cell's response when presented with both motion patterns independently. In a recent paper, Graziano et al determined that statistically the separation of MSTd neurons into single, double, and triple component subclasses was arbitrary. Instead of distinct groups of cells tuned to particular elementary flow components, MSTd may have a continuum of neurons selective for various combinations of motion types. The poor position invariance results found in multicomponent cells when compared to single component cells can also be explained using this new interpretation of MSTd. When Graziano et al tested for position invariance using the proper stimuli these neurons that had poor position invariance now had good performance.[106]

Knowing that MST receives the bulk of it's input from MT, a general model was developed that suggested that many of these directional units with small receptive fields in MT form units that funnel information into MST. MST then forms its invariant motion pattern preferences and large receptive field from the inputs of MT cells with receptive fields in various parts of the visual field. This led to the assumption that MSTd cells could be responsible for analyzing wide field movements that commonly occur with ego-motion. If so, do these neurons, like the computational models discussed previously, also decompose the optic flow patterns into their elementary components?

This decomposition hypothesis states that all complex motion patterns can be decomposed into expansion, rotation, and translation. One possible way that MSTd can accomplish this decomposition is if it processes each elementary

flow component in a different neuronal channel. In this scheme, the cells that are selective for multiple motion components would be found on the lower level of the hierarchy, while neurons responding to one motion type represent the final analysis stage.

In a 1992 paper Orban et al. attempted to test this hypothesis by asking whether neurons in MST could extract expansion from a spiraling pattern that was composed of expansion and rotation. The neuron's response to this pattern was compared to its response to a purely expanding pattern with the same degree of expansion.[107] If the responses were similar, then it could be said that this neuron was decomposing the flow presented into its elementary components. However, this was not the case. In this experiment, the cell did not respond favorably to the spiral. By finding neurons that responded to a continuum of directions, expansions, contractions, rotations and combinations of flow (spirals), the Graziano experiment also disproved this theory of decomposition in MSTd.[108] While the early experiments by Duffy and Wurtz seemed to support this decomposition theory, later studies by the same group also concluded that MSTd neurons were not multicomponent, but instead prefer one motion stimulus.[109,110] If these neurons don't decompose optic flow patterns what could they be doing? One general theory has MSTd neurons processing all types of visual motion via templates. These templates are similar to those neural network models discussed in Chapter 2 that were involved in direction of heading estimation. Much like these artificial networks of neurons,

MSTd may be composed of a variety of templates representing all possible combinations of complex flow patterns. The appropriate neurons respond when the animal is confronted with the corresponding flow. These templates, as you will remember from our earlier discussion of optic flow, recognize the flow patterns that arise when observers move about in the environment. Because of this similarity in response to the types of flow produced by observer translations, along with its large receptive fields, strong responses to larger (arguably representing spatially closer stimuli), and dependence of vector direction, MSTd has been implicated as the region in primate brain where direction of heading computations are processed.

FUNCTIONAL ROLE OF MSTd

Given that the study of MST is still in its scientific infancy (~20 years old) , its role(s) if any, in many perceptual and behavior tasks is not yet known. However premature, its behavior when confronted with complex motion patterns has lead many to believe that MSTd is the center for self-motion.

There are many indications that MSTd is involved in visually guided navigation. In chapter one it was established that navigation is trivial if the eyes are held fixed in the head. It is the added eye rotations that occur when observers are free to look about in their environments that cause this problem to become a more complex one. When considering the problem of gaining heading information from optic flow one has to remember that heading is represented in

retinal coordinates. The locations of field singularities representing the observer's destination changes with eye movements. Therefore, if MSTd is involved in this estimation it must take into account eye position information. While the computational models proposed many possible solutions to this problem utilizing both retinal and extra-retinal flow, psychophysical experiments reviewed in the last chapter revealed that extra-retinal signals play a very crucial role in factoring out the flow contribution of eye rotations. When the observer moves his eyes, the effect of eye rotation on the flow field is invariant to environmental structure. An extra-retinal signal could represent the eye movements contribution to the flow field. If this added rotational flow is subtracted from that of the retinal flow field, the representation of the optical flow field independent of eye movement remains. The direction of heading can now be clearly determined. This factor gives a strong indication that MSTd is indeed involved in self-motion analysis.

When considering the flow fields generated by primate motion in the world, we should also take into consideration that we tend to move forward, therefore most of the optic flow stimulation we would receive would contain expanding patterns. We rarely move backwards so we would expect that a region processing ego-motion information would be underrepresented with cells tuned to this motion type. In the electrophysiology literature we find that most laboratories have found a significantly higher percentage of MST cells

preferring expansion patterns than any of the other radial motion types. This is in line with our natural visual experience.[111,112]

Another indication of MST's ego-motion involvement is its dependence on the global motion pattern in the scene. It has also been shown psychophysically that subjects relied heavily on the global pattern of the velocity field when making heading judgments whether or not the focus of the expansion was on the screen. Their performance was impaired when the orientations of the vectors were randomized not when their magnitudes were nonuniform. These results suggest that instead of "looking" for the singularity in the field, as some have proposed, the brain must be using the spatial arrangement of the vectors to draw some conclusion as to where the observer is heading.[113]

In order for this scheme to work, the anatomical area involved must not only rely on vector orientation it must have a receptive field large enough so that it can gather a representative sampling of motion activity in the visual field. Figure 5 shows the large field stimulation of optic flow field resulting from an observer's movement into the page. Area V1, primary visual cortex, although sensitive to motion has a small receptive field represented by the small square. This area is much too small to successfully analyze the flow field. Further along the extra striate pathway, the receptive field sizes are a bit larger in MT, the middle temporal area. However as the circled area in the figure shows too much of the flow field is ignored for this area to be sensitive to the optic flow. MSTd neurons have large receptive fields, indicated by the dashed square that

usually include the fovea. These receptive fields are large enough (40° to 100° wide) to include a large fraction of the optic flow stimulus.

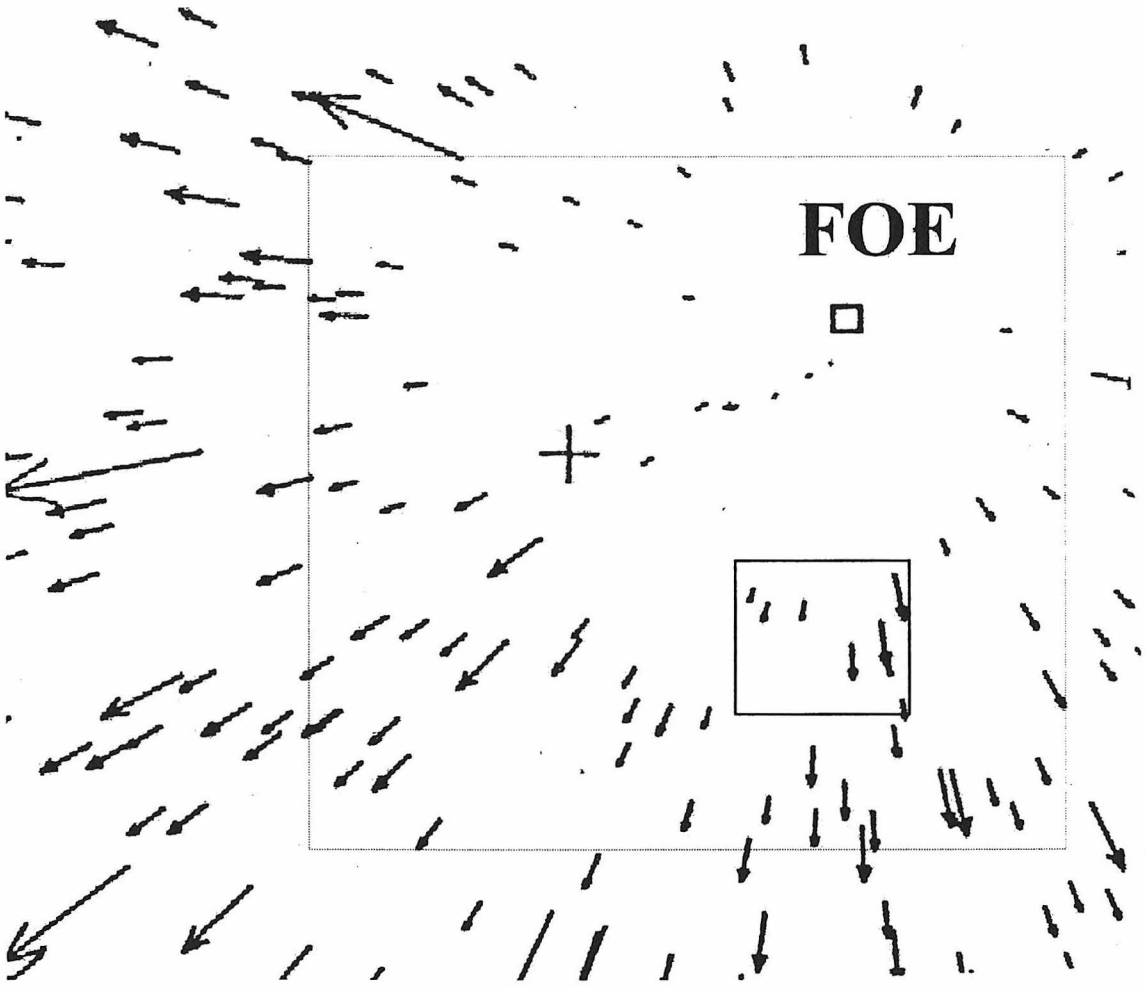
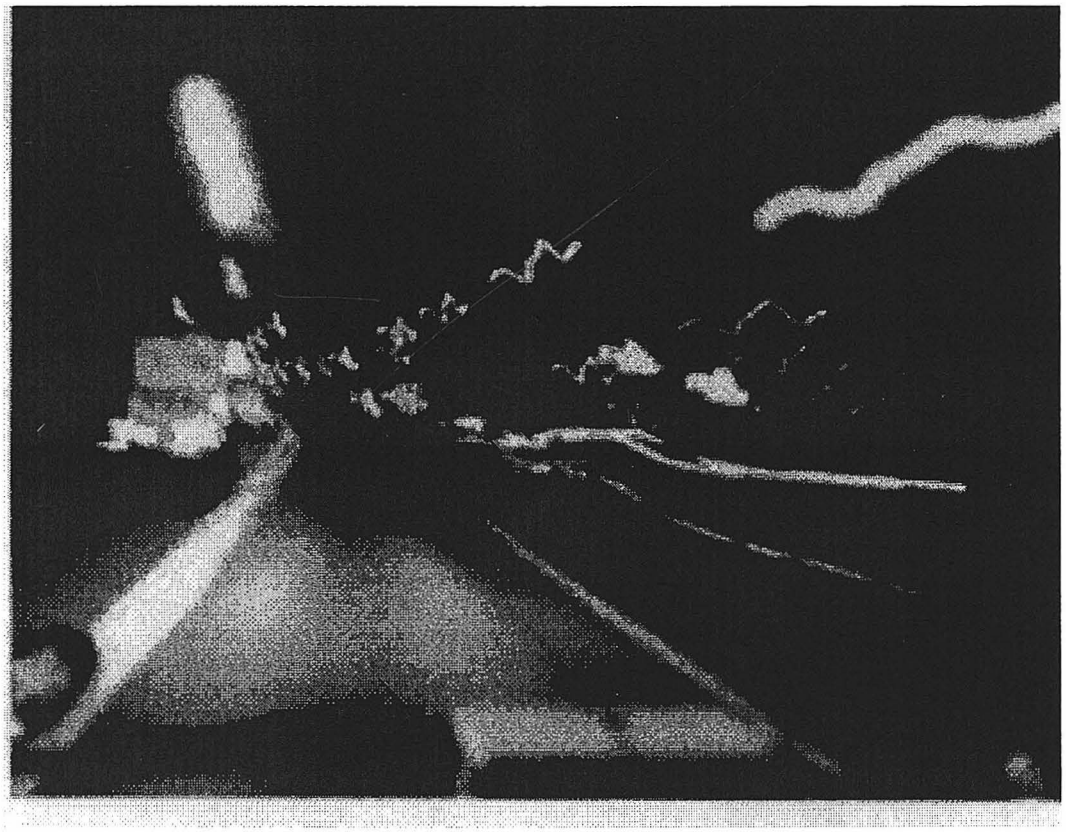


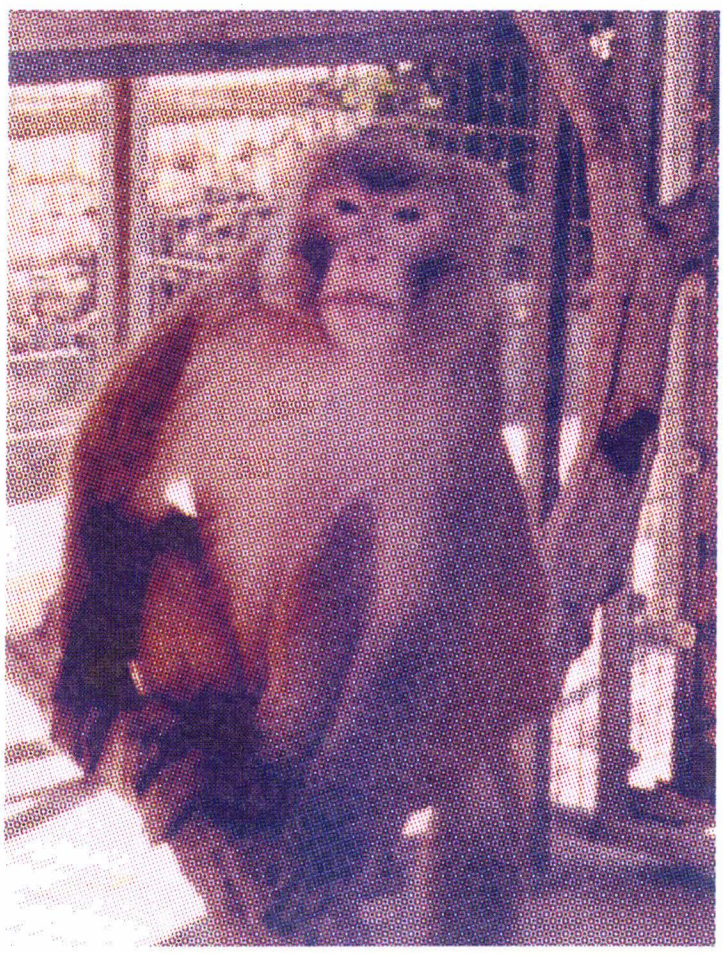
Figure 5: This is a symbolic rendering of average receptive field sizes in the visual areas. The first small black square, represents V1, the second green box MT, and the large red hashed box MSTd. Only MSTd has receptive fields large enough to encompass a wide sample of the optic flow field to give an approximation of heading. *Adapted from Duffy and Wurtz 1992?*

A fairly strong case can be made that MSTd processes optic flow. However, several other roles for MST are also possible including vection, structure from motion, and "reference signal." The available evidence cannot rule out a role for this region in processing optical flow information. It has extra-retinal smooth pursuit signals that are independent of visual input, its responses depend on the global motion pattern in the scene, and it has a receptive field large enough to encompass a large fraction of the flow field. However promising these characteristics may be we have yet to show conclusively that MSTd can determine the direction of heading from optic flow stimuli. It is likely that MST plays a major role in the processing stream involved in recovering data encoded in the optic flow field.

Although we do know that MSTd neurons respond to stimuli consistent with simulated observer translations and rotations, and that it codes for extra-retinal pursuit signals, it is not clear how these two characteristics interact to possibly reflect observer heading. In the next section we will address this question. First by directly measuring MSTd neurons responses to optic flow fields in the presence of pursuit eye movements in Chapter 5 and then by correlating these results with human abilities to compensate for shifted foci caused by eye movements in expanding, rotating, and finally spiraling patterns in Chapter 6.



This is an all too familiar scene for the commuter. A time lapse photograph captures the streamming lights which seem to both expand and curve indicating the drivers destination point.. At some point he undoubtably made an eye movement to check the speeding truck in the next lane. How does the brain account for these eye movements and will it respond similarly when this optic pattern contains rotations such as this one?



-Betty Gilkin

We recorded from Spot's brain to see if MSTd neurons compensate displacements in the optic flow image caused by eye movements in Chapter 5. These results set the basis for the human psychophysics experiments in Chapter 6 which attepmt to correlate human perceptions with monkey physiology.

Part II: MSTd and Heading Perception

Chapter Five:

Mechanisms of Heading Perception in Primate Visual Cortex

Chapter Six:

Comparisons of Eye Pursuit Effects on Expanding and Rotating Motion Patterns

CHAPTER 5:
Mechanisms of Heading Perception in Primate Visual Cortex



This Japanese macaque successfully navigates through the thick underbrush. How does her brain accomplish this task? Are MSTd neurons actively helping to compensate for displacements caused by eye movements?



-Fritz Goro

Electrophysiology allows us to easedrop on the activities of individual neurons and categorize their responses to specific stimuli. In this case we are interested to know how MSTd neurons react when simultaneously presented with optic flow patterns and pursuit eye movements.

ABSTRACT

When we move forward while walking or driving, what we see appears to expand. The center or focus of this expansion tells us our direction of self-motion, or heading, as long as our eyes are still. However, if our eyes move, as in tracking a nearby object on the ground, this disrupts the retinal image and shifts the focus away from the heading. Neurons in primate cortical area MSTd respond selectively to an expansion focus in a certain part of the visual field, and this selective region shifts during tracking eye movements in a way that compensates for the retinal focus shift. Therefore, these neurons account for the effect of eye movements on what we see as we travel forward through the world.[1]

[1] Portions of this chapter appear in DC Bradley, MA Maxwell, RA Andersen, MS Banks, KV Shenoy, ***Science*** Sept 13, 1997.

5

When we move along a straight path, the retinal image appears to expand, creating a vector field on the retina in which all vector directions point away from the focus of expansion. When the eyes are still, this focus corresponds to the direction of self-motion (the heading), which humans can easily identify.[114,115] When the eyes move, the problem becomes more complicated. If we turn our eyes leftward to maintain fixation on an object to the left of our motion path, a rightward laminar flow component is added to the expanding retinal field. This combined field is similar to the original expansion field (when the scene contains little depth variation), but the apparent focus position becomes shifted to the left of the heading (***figure 1***).

Humans can still estimate heading during pursuit eye movements, showing that they can correct for this shift. Recent psychophysical experiments have shown that this correction requires eye movement.[116] One might therefore expect the brain site(s) responsible for heading computation to process smooth pursuit eye- movement signals as well as optic flow.

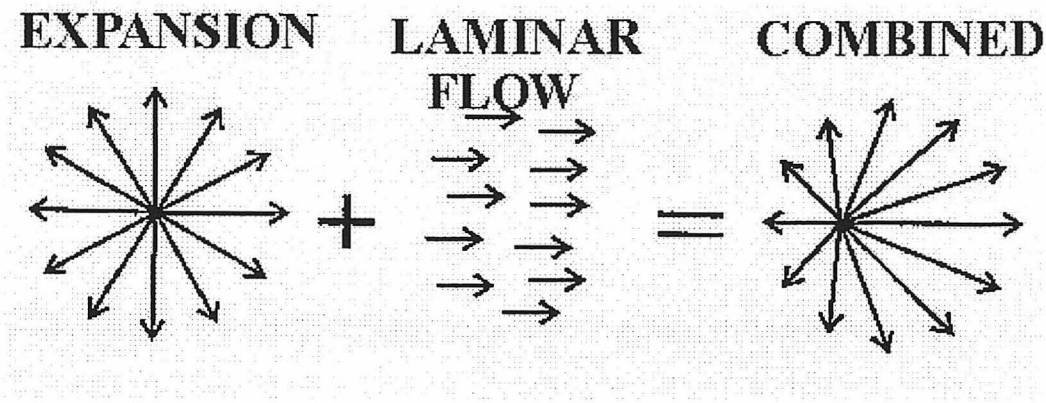


Figure 1. When we move forward, the visual world appears to expand. If the eyes are still, the focus position tells us our direction of heading. However, leftward eye movement adds rightward motion to the retinal image, which shifts the focus. To recover the heading direction, we must correct for this focus shift

With this in mind, we examined the dorso-medial superior temporal area (MSTd), because its neurons are responsive to optic flow stimuli (e.g., expansion) as well as smooth pursuit eye movements Komatsu and Wurtz, 1988, Newsom et al, 1988}.[117,118,119] Many MSTd cells are also selective for the position of the focus of expansion (Duffy and Wurtz, 1995).[120] Our goal was to determine how optic flow and eye-velocity signals might be used in area MSTd to compute the direction of self-motion.

We trained a rhesus monkey to fixate a point on a computer screen. The monkey was seated in a chair with his head fixed and faced a 100° x 100° projection screen. After maintaining fixation with a 5° x 5° window for 3 sec, the monkey was rewarded with a drop of water. The position of his eye was closely monitored with a scleral eye coil.[121] The point was either stationary or moved at a constant velocity of 15.7°/s). While the monkey fixated, we showed a large, expanding random-dot pattern

for one second. These expanding random dot fields were generated by simulating the approach to a wall at 38 cm/s at a distance of 57 cm. To limit acceleration cues, dot lifetimes were kept at 300msec, after which they were renewed at random locations in the field. The stimulus was 50° x 50° and contained 77 dots. The position of the focus in this expansion was varied along an axis to simulate different directions of self-motion, or headings in 10 step intervals from -40° to 40° along an axis parallel to the neurons preferred pursuit direction. These distances were relative to the center of the stimulus which was itself centered on the neurons spatial receptive field. The neurons' spatial receptive field and preferred pursuit timing were determined having the monkey follow a point moving at 0°, 45°, 90°,... or 315° . The direction eliciting the strongest response was taken as the preferred direction, the opposite direction was labeled the antipreferred direction in preliminary tests (figure 2).

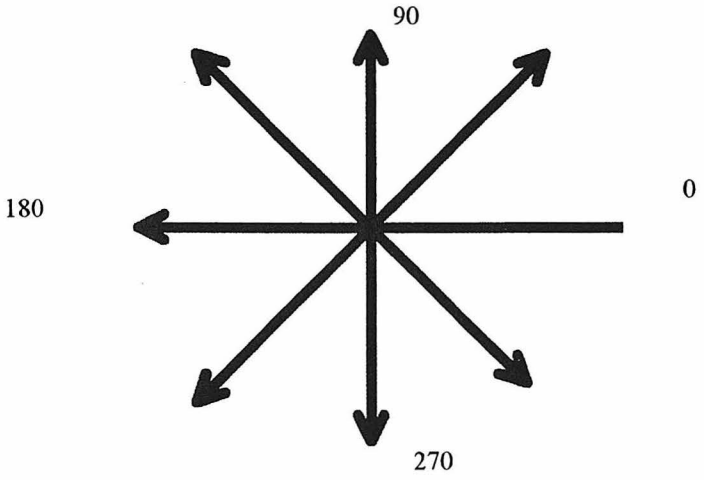


Figure 2: The monkey was trained to pursue along one of eight directions. In this case, the monkey will pursue aong the 0-180° axis shown in red. Since the pursuit is from right to left, if the neuron preferred leftward eye movements the 0° axis was taken as the anti-preferred direction.

During the stimulus presentation we recorded single-neuron activity with a microelectrode inserted in MSTd cortex. These electrodes were varnish coated tungsten microelectrodes advanced dorsoventrally through the dura and into MSTd.

We identified MSTd by its receptive field size (most were >50° wide and crossed the vertical meridian), flow preference (e.g. expansion, roatation), position invariance, and smooth pursuit activity. The optic flow preference (i.e., expansion, contraction or rotation) of each MSTd cell was first determined). Spike times were stored on a personal computer for subsequent analysis. All data are expressed as the mean firing rate during the middle 500 msec of a 1 second stimulus presentation period. The results here are based on a sample of 139 neurons from one hemisphere and were corroborated by recent data from a second animal (n=18).

After the cells motion preference was determined the following tests were conducted. First, while the monkey fixated a stationary point, we recorded the cell's firing rate as a function of the position of the flow focus on the screen (the simulated heading). All stimuli were presented in pseudorandom order. This allowed us to measure the neuron's focus tuning; that is, its response profile as a function of heading. These tuning curves were usually well-defined and roughly sigmoidal or gaussian in shape. The tuning curve peaks were fairly evenly distributed from -40° to 40°, suggesting a continuum of preferred headings.

When the eyes are fixed, the heading is given by the retinal focus position. Therefore, we cannot tell whether the fixed-eye focus tuning curves represent heading or simply the position of the focus on the retina. To make this distinction, we showed the same expanding patterns during a 15.7°/s smooth-pursuit eye movement. The eye movement was made in the neuron's preferred direction or the antipreferred (opposite) direction in order to elicit the largest effect. Data were recorded over a 500 msec

interval during which the eye moved 8°. The average eye position during the recording period was the same as in the fixed-eye experiment. However, the eye's instantaneous velocity displaced the apparent focus by 30° in the direction of the eye movement. The simulated heading in screen coordinates remained unchanged.

If MSTd activities reflect the heading, we expect their fixed- and moving-eye focus tuning to be the same when expressed in screen coordinates. Since the monkey's eyes and head were in a constant position(except for the small eye displacements during pursuit tasks) we cannot tell whether MSTd cells are coding for heading in reference to the eye, head, body, or the world. Screen coordinates was adopted to account for operational reasons. Our results simply imply that these cells are accounting for the eye movement. On the other hand, if their response is determined solely by the pattern of retinal image motions, we expect the tuning curves to be the same when expressed in retinal coordinates. We found both types of cell, as well as intermediate types. Retinal cells were arbitrarily defined as those shifting by -20°,-10°, or 0°; intermediate neurons as shifting by 10° or 20°, and heading (screen) neurons as having a 30°, 40°, or 50° shift. We found approximately 42%,31%, and 27%, respectively. Here the shift estimate was based on maximum cross correlation between the fixed and the moving eye curves. ***Figure 3*** shows a neuron for which responses were similar in screen coordinates. In this cell, an eye movement in the preferred or antipreferred direction caused the focus tuning to shift by approximately 30° in retinal coordinates (top right panel) such that the two moving-eye fields and the fixed-eye field were nearly superimposed when plotted in screen coordinates (top left).

Thus, activating this neuron reflects the position of the screen focus rather than the retinal focus.

The above experiment suggests that an eye movement signal is used to shift the retinal focus tuning. This is because the expansion stimulus is two-dimensional and thus devoid of retinal cues, such as motion parallax, that might give information about the rate of eye.[122,123] To prove that eye-movement signals are used, we presented a retinal stimulus virtually identical to that in the eye movement experiment above, but with the eyes stationary. This stimulus was achieved by having the animal fixate a stationary point while moving the expansion stimulus, including its border, in the opposite direction of the simulated eye movement. It is important to note that the retinal image over time is the same in this and the real eye movement condition; the only difference is that the eye moves in the real movement condition and does not move in the simulated movement condition. There was a slight difference at eccentric positions due to tangent error on the screen. Dot speeds for the pursuit and stimulus in these cases were ~8% at 12.5 deg eccentricity, ~20% in the corner at 35% eccentricity, and 0 in the center. Therefore, the real and simulated pursuit conditions differ slightly only in terms of the distribution of speeds across the retina. In most cases the simulated pursuit experiment caused no shift in the retinal focus tuning (***figure 3***, bottom right). Therefore, the focus tuning shifts observed in our experiments can only be attributed to the influence of an extra-retinal eye movement signal. The effect of

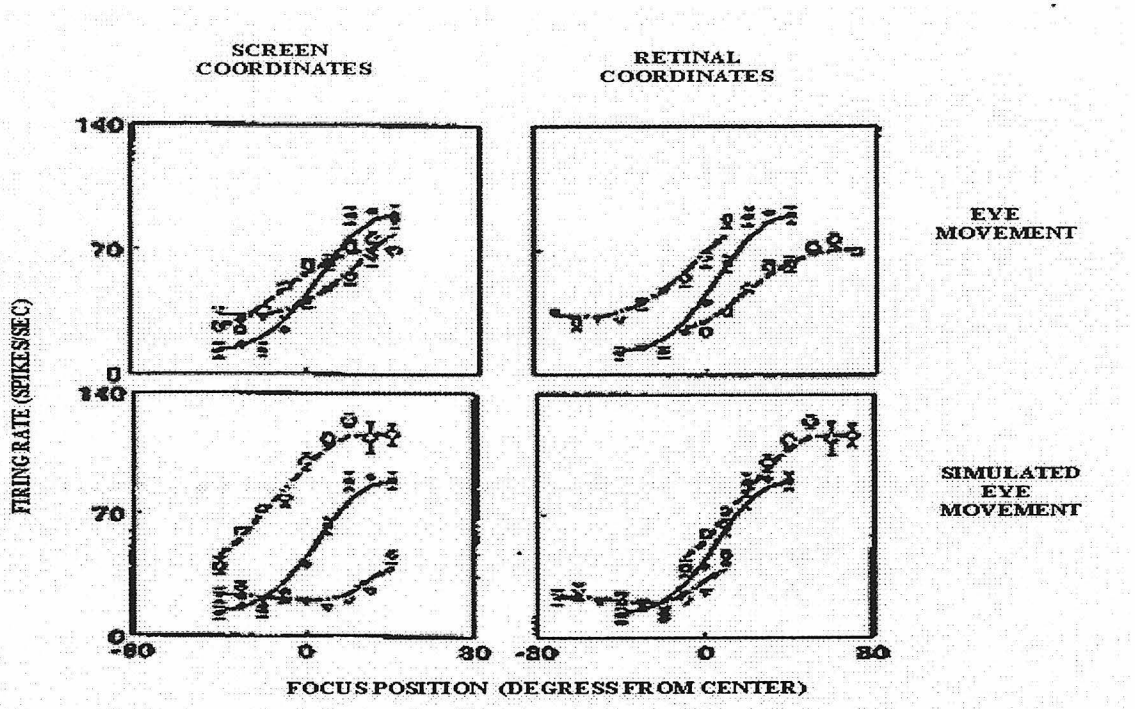


Figure 3. An MSTd ``heading cell." In all panels, the solid lines/solid circles represent the fixed-eye focus tuning (identical in all 4 graphs), dashed-lines/open squares are preferred-direction eye movements (real or simulated), and dot-dashed-lines/open triangles are antipreferred-direction eye movements (real or simulated). Top row: real eye movements. Bottom row: simulated eye movements. Left column: screen coordinates. Right column: retinal coordinates. Data in the left and right columns are identical, except pursuit curves in the right column were shifted by ± 30°relative to screen coordinates (thus giving retinal coordinates). The moving-eye focus tuning curves align in screen coordinates (top left panel) and thus encode the direction of heading. However, for simulated eye movements the fields align in retinal coordinates (bottom right panel). Smooth curves are 5-point moving averages of the data. Data points are means SEM for 4 replicates, where each replicate is the mean firing during the middle 500 msec of the stimulus presentation interval.

This signal in bringing focus tuning curves into screen coordinates is seen by comparing pursuit curves between the lower and upper left panels: in the simulated case, the curves are not aligned in screen coordinates (lower left) whereas they are in the real pursuit case (upper left).

To summarize results for the entire neuron sample, we measured the cross-correlation coefficient (Rc) between fixed- and moving-eye focus tuning curves for a variety of relative shifts between the two curves. To compute Rc for a given relative

shift between curves, the responses on one curve were correlated against the responses on the other curve, pairing by X-axis value. Only overlapping regions of the curves could be cross-correlated .MSD was computed as the mean squared difference between corresponding data points on the two curves, again, only for overlapping regions. A High Rc value indicates that the two curves are well aligned at a given relative shift. When pursuit eye movements were simulated, the optimal shift (that maximizing Rc) was near zero with respect to retinal coordinates (***figure 4a***). In contrast, during real eye movements, the relative shift was ~15° away from retinal coordinates and toward screen coordinates. This is not to say that all neurons shifted by 15°; instead, optimal shifts were relatively evenly distributed between -20° and 50°(***figure 4c***). By comparison, this distribution for simulated eye movements was heavily stacked in the region of zero shift. Thus, the effect of actual pursuit was to cause many neurons to shift their focus tuning toward a screen coordinate frame. Results were similar when the optimal shift was calculated by minimizing the mean squared difference (MSD) between fixed- and moving-eye tuning curves (***figure 4b,c***). Also, results were similar for preferred- and antipreferred-direction eye movements (antipreferred data not shown); the shifts were opposite in the two cases (see ***figure 3***), require pursuit compensation. Another explanation, however, is that the distribution of shifts reflects the transformation from retinal to screen coordinates. In this case, one would expect to

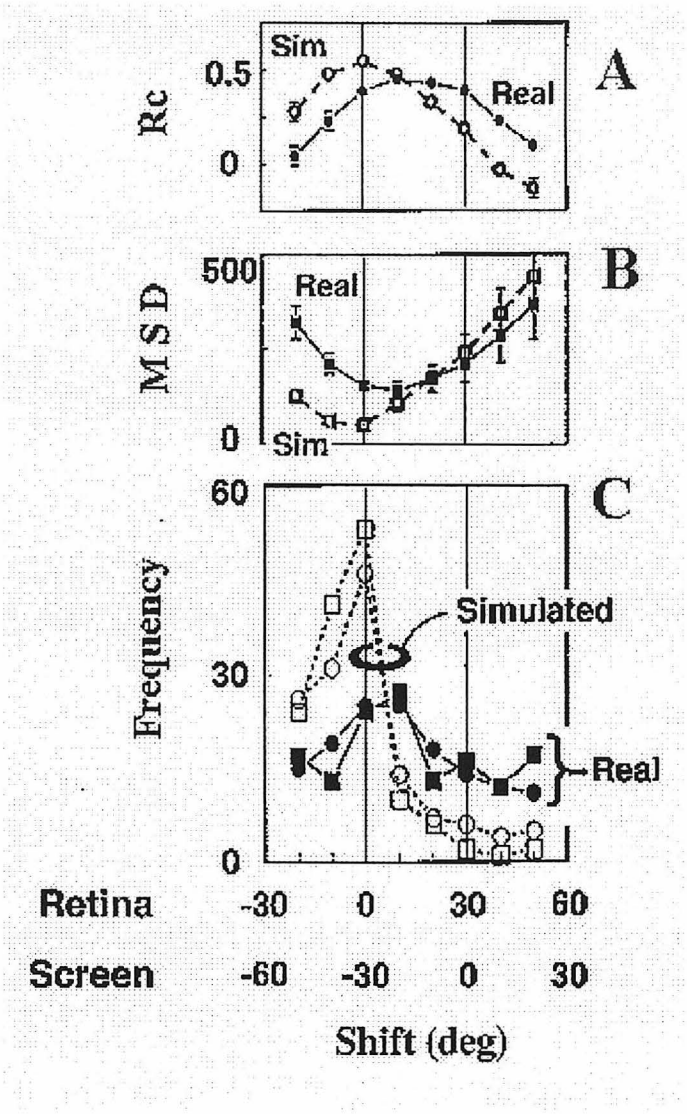


Figure 4. Population data representing the entire MSTd sample (n=139). {X-axis} represents relative shift between fixed- and moving eye focus tuning curves. Each panel compares results for real pursuit and simulated pursuit. **Panel A**: Cross-correlation coefficient (Rc). For each relative shift, a correlation was done between the overlapping regions of the two curves. High Rc values imply good alignment on the {X-axis}. One cross-correlogram (Rc vs. shift) was defined for each neuron and for each pursuit direction; cross-correlograms were then averaged over cells to form the data of this panel. **Panel B**: mean squared difference between focus tuning curves (MSD). Averages computed as for Rc (above). **Panel C**: Frequency distribution for ``optimal" relative shift, defined in terms of maximal Rc or minimal MSD. One optimal shift value was defined for each cell (for the preferred pursuit direction); the histogram reflects the frequency of each optimal shift. In all panels, circles = Rc data, squares = MSD data; solid symbols = real eye movement, open symbols = simulated eye movement. Panels A and B: data are means\pom sem (n=139).

find neurons representing various stages of the coordinate transformation; i.e. non-shifting cells (retinal coordinates), shifting cells (screen coordinates), and possibly cells corresponding to intermediate stages of the transformation. Presumably, heading judgments would be based on the activity of heading cells rather than on those taking part in the transformation. However, it is possible that all MSTd activities are sensed at once, conveying a mean shift of about 15°(***figure 4c***); this would be consistent with

psychophysical experiments showing that subjects may only partly correct for pursuit eye movements when judging stimulus motion in screen coordinates.[124,125]

That MSTd may convert retinal to screen coordinates is supported by the finding that in most non-shifting neurons, response amplitude was modulated by pursuit. Heading cell receptive fields also showed gain changes. In fitting our model (***figure 5***) to the heading cell data, these gain changes were taken into account, along with the receptive field shifts (amplitude change: 25±3\% on average; ***figure 5a***). It is uncertain whether these gain changes encode information about heading: it is possible that they simply average to zero. If the output of two such neurons were summed the resulting focus tuning could shift if the two input tuning curves were offset relative to each other. To test this idea, we modeled heading cell focus tuning curves as the sum of two mutually offset sine functions (representing the non-shifting cells). By changing the amplitude of the sines, it was possible to recreate the measured heading cell tuning curves consistently (mean $r^2 = 0.7 \pm 0.03$ when all heading cell tuning curves were fit with this model). ***Figure 5b*** shows an example. The shift of this cell's tuning curve occurs because its two input functions are offset relative to each other, and the gain changes on these functions alter their relative inputs to the heading cell. Thus, our modeling suggests that heading (shifting) cells could be built up from non-shifting, retinal cells in area MSTd. The Figure 3 data were pooled from neurons tuned not only for expansion (41\%), but for contraction

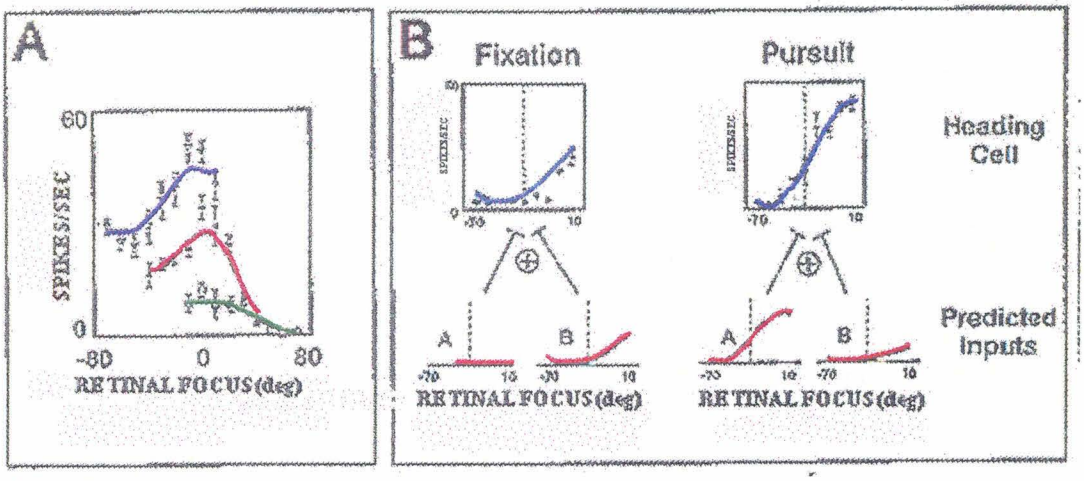


Figure 5. Panel A: Example of a retinal (non-shifting) neuron whose response amplitude is modulated by pursuit. The three curves, corresponding to stationary fixation and opposite directions of pursuit, all peak at 0, but their amplitudes vary substantially. This type of cell could serve as input to the heading (shifting) cells. Panel B: Example of a heading neuron and how it might be constructed from retinal neurons. The upper graphs show the neuron's measured focus tuning, during fixation (left) and preferred-direction pursuit (right). The neuron shifted its retinal focus tuning during pursuit in such a way as to compensate for the retinal focus shift induced by that pursuit. Circles: mean response; curves: model fit. Lower panels: predicted input functions. Each function is characterized by 3 sine-wave parameters and multiplied by a gain; two functions are summed to make the focus tuning curve of a heading cell. All parameters were adjusted by nonlinear regression to fit the data (upper panels). The focus tuning shift during pursuit was achieved by increasing the gain on function A while decreasing the gain on function B. The sine-wave parameters (other than gain) were identical for the fixation and pursuit conditions; only the gains were adjusted to simulate the focus tuning shift. The gain-modulated sine functions resemble neurons in sample which have gain-modulated (non-shifting) focus tuning.

(33\%) and rotation (27\%) as well. The data were combined because the results from the three cell types were nearly identical . Thus, for expansion, contraction and rotation cells, focus tuning shifted during eye movement (compared to simulated eye movement) by 18± 3°, 15± 3°, and 17±4°, respectively, in all cases toward a screen coordinate frame. This is remarkable because expansion, contraction, and rotation patterns require focus tuning shifts in different directions to compensate for focus shifts during eye movements. For example, an eye movement to the left shifts the retinal focus of an expansion to the left (***figure 1***), but the retinal focus of a clockwise rotation

is shifted downward (***figure 6***). The expansion cell would thus require a leftward tuning shift and the rotation cell a downward shift to compensate for the retinal focus shift. This is indeed what MSTd neurons appear to do, suggesting a general mechanism which compensates for the effect of pursuit eye movements on various types of retinal flow, not just expansion.

In conclusion, many MSTd neurons are tuned to the position of the focus in an optic flow pattern (e.g. expansion, contraction and rotation). In addition, many neurons shift their retinal focus tuning during eye movement in the same direction as the shift in the retinal focus induced by that movement. This focus tuning shift can only be attributed to an eye-movement signal to MSTd, because an identical retinal stimulus in the absence of eye movement produces no such shift. In the case of an expansion stimulus, focus tuning shifts are in the appropriate direction for encoding the heading. However, the shifts for rotation and contraction cells may indicate a more general phenomenon of perceptual stability in the face of retinal motion due to smooth pursuit eye movements. Thus, for instance, when the eyes track across a rotating wheel, the wheel does not appear to move up or down. Thus, MSTd may play a general role in using eye movement signals to compensate for self-induced image motion---that is, the motion we see because of the eye movements themselves. One important outcome of this compensation is the ability to compute the direction of self-motion.

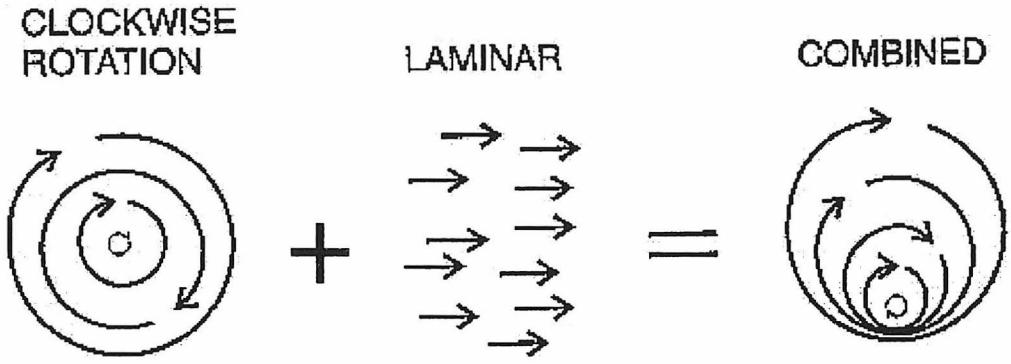
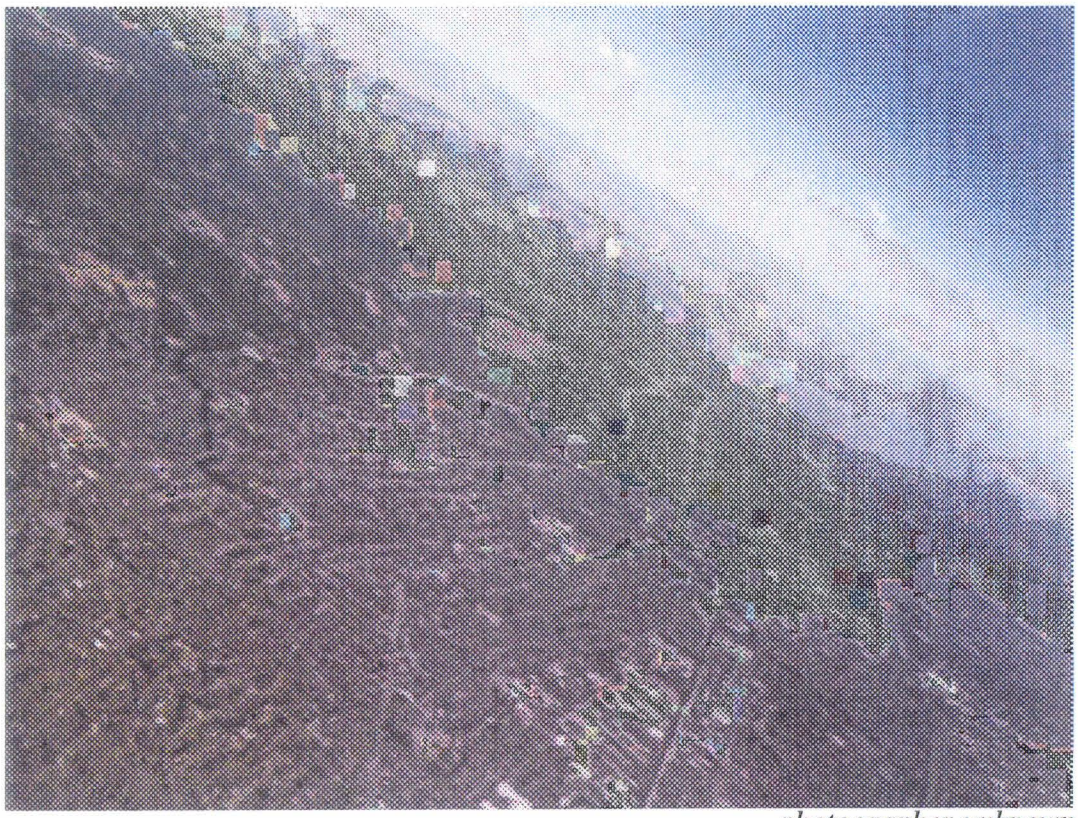


Figure 6. The focus in a clockwise rotating pattern shifts downward during a leftward pursuit eye movement, which produces rightward laminar flow. To correct for this shift, clockwise-rotation cells must shift their retinal focus tuning curves downward. This is equivalent to the focus tuning shifts of expansion cells, which go in the direction of eye movement, because in both cases the neurons are changing their flow preference to accommodate more rightward-linear motion.

We now have strong evidence that MSTd is actively involved in the calculation of heading and that this calculation is compensating for eye movements. Although this is the case physiologically there is no evidence linking the behavior of MSTd neurons to similar perceptual correlates in the human. Are our brains similarly accounting for the eye movements by making parallel and perpendicular compensations? Also can we use purely rotatory or spiraling patterns to perceive heading? The next chapter will address psychophysically if we are also able to accurately judge the locations of the focus positions under these conditions with both real and simulated eye movements. If we show similar behaviors, this would support the notion that shifting receptive fields in MSTd are associated with our perceiving focus position in the world when our eyes are moving.

CHAPTER 6:

Comparisons of Eye Pursuit Effects on Human Perceptions of Expanding and Rotating Motion Patterns



-photographer unknown

The landscape appears to rotate and spiral as the pilot prepares for landing. Are the optic flow patterns he experiences while banking (rotations) processed in the same manner as those he experiences while moving forward (expansions)? Can our perceptions of optic flow be predicted by the behavioral activities of macaque MSTd neurons?

6

Most theoretical and psychophysical studies of self navigation from optic flow stimuli utilize Gibson's notion that the important cue used by observer's as they move about in the world is the focus of the expanding motion pattern on the retina).[126,127,128] When we move our eyes the focus of that expansion (FOE) shifts away from the destination point in the direction opposite the eye movement. Much work has been done to remove the laminar motion contribution to the retinal image resulting from these eye movements.

Area MSTd in the macaque has been targeted as the area playing a principle role in heading estimation from optic flow. Recent findings by Bradley et. al, support this theory. In that study it was found that MSTd neurons use an extra-retinal signal to help compensate for retinal focus).[129] This corrective action shifted the focus away from retinal coordinates and towards a world coordinate frame. These neurons exhibited receptive field shifts irrespective of flow preference although each optic flow

pattern requires a different direction of shift to obtain a world coordinate frame. An example of this difference can be seen when expansion and rotation stimuli are compared (figure 1). If a leftward eye movement is executed (resulting in a rightward laminar flow) the focus is shifted towards the left on the retina- a shift that is parallel to the eye movement. If the same rightward laminar flow is added to a counterclockwise rotating stimulus this results in a focus that has been shifted downward with respect to the original focus. The corrective shift in this case is perpendicular to the eye movement. Therefore to make these compensatory shifts when there are eye movements, MSTd must be capable of making both parallel and perpendicular shifts.

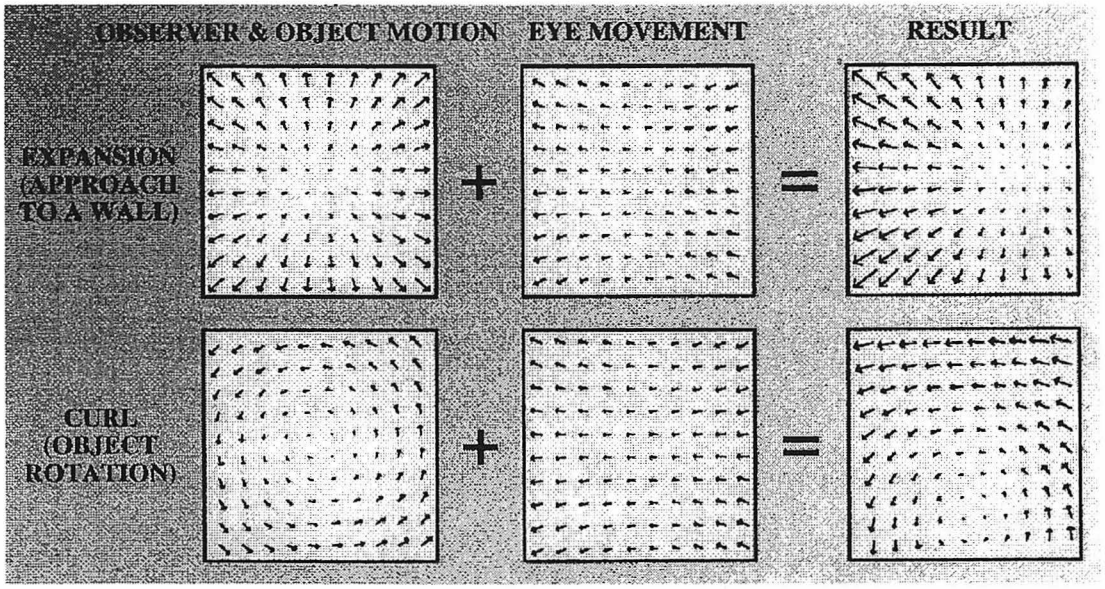


Figure 1a: Adding a rightward linear flow (leftward eye movement) to an expansion pattern causes the focus to shift to the left-parallel to the eye movement. ***Figure1b***: For rotations this eye movement induced shift is down perpendicular to the eye movement.

Interestingly MSTd neurons seem to be capable of making accurate estimations of focus position from purely rotary stimuli as well as from the expanding ones. While the focus of an expanding pattern is used to denote the instantaneous direction of

heading of an observer and its relationship to the observer is well understood, the same can not be said of the foci of rotary stimuli. What purpose(s) could these brain cells that correctly estimate the foci of rotary stimuli have since we rarely see rotations? Are these neurons also involved in navigation or do their function lie else where?

There are a few reasons for the presence of these rotation detectors. One could be that these neurons help in stabilizing rotating images on the retina. Imagine that an observer tracks a ball across a rotating tire. The eye movement would cause the center of the tire to shift upwards or downwards depending on the direction of pursuit and rotation. Regular terrestrial movements often give spiralling or rotary optic flow patterns if the observer fixates a mark on the ground while moving forward. We can also picture the view a hawk or pilot flying above the ground plane would have as it looks down to the surface (see opening picture). Both would experience rotary optic flow patterns while banking in an attempt to capture prey or land on an aircraft carrier. Similarly then, these same rotation detection neurons could serve a dual function by also aiding the observers in orienting themselves when moving about in the world.

A more novel idea is that these cells are also involved in recovering heading. David Bradley has proposed a spiral space model where expansion, contraction, spiral, and rotations sensitive neurons in MSTd determine an observer's direction of heading in a 3-D environment (figure 2). These neurons would act as templates responsible for locating the focus of optic flow patterns.



Figure 2: The spiral space theory has heading being determined in any 3-D environment from a set of MSTd neurons receptive to a continuum of spiral patterns. The two axes involved in this study were the expansion/contraction axis and the clock-wise/counter-clock-wise axis.

In a population of these neurons, the cell having the strongest response would represent the heading direction. This detection process takes into account MSTd neurons' focus preferences shift with eye movements. A simple example could be an observer pursuing a ball leftward on a ground plane normal to the direction of heading. The observer sees a rotation pattern, but the leftward eye movement would cause a downward shift of the focus position. Heading can be deduced from a cell that has a

preference for leftward linear motion (focus below the horizon) when the eyes are still, but shifts to a central focus preference during leftward pursuits. The signal from this cell would report this leftward flow thereby indicating a heading to the right of the line of sight.

However plausible these suppositions for the purpose of MSTd's rotation selective cells, it must first be determined whether or not human brains can also compensate for shifts in the focus position of rotating patterns when the eyes are moving. Here we compare the effects of pursuit eye movements on human perceptions of focus position when viewing expanding and rotating optic flow stimuli.

Subjects

Six people participated in this study four male and two female. Three were authors (MM,JC,RA) and three were naive volunteers. One subject (MH) was paid for her participation. All had corrected 20/20 vision in the eye used for the study.

Instrumentation

Stimuli were generated using a Macintosh 7500 computer using MATLAB. Images were presented on a back projected DA-LITE DA-PLEX Picture Window rear projection screen with a GE Imager 410 model AVDU4900 Data Unit projector unit.

Stimuli

Stimuli were similar to that used by Bradley et al. (figure3).[130] And consisted of expanding and rotating (curl) random dot patterns subtending 40°X 40°. The speed gradients were set at .65°/sec/sec. There were 200 dots presented with lifetimes of 300 msec and the stimulus was presented for 500 msec.

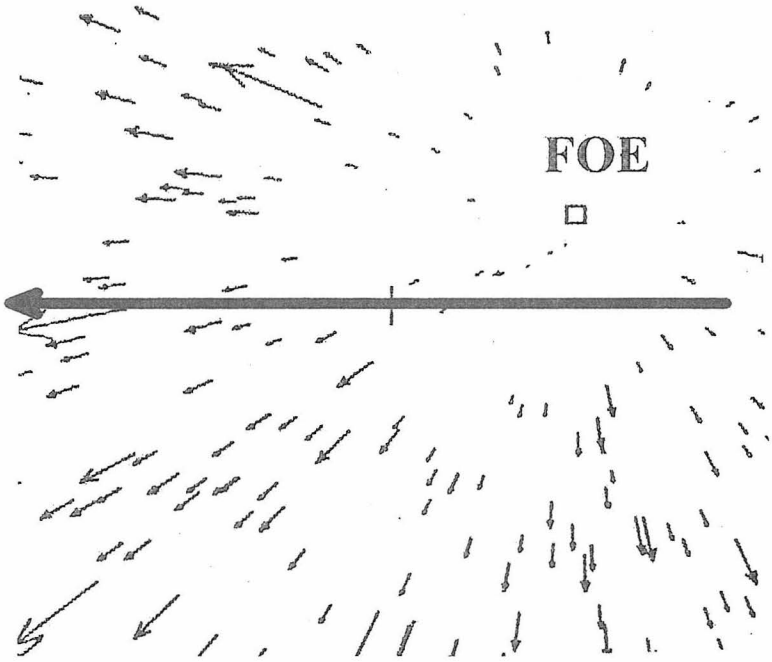


Figure 3: Subjects viewed an optic flow pattern and were instructed to either follow the cursor with the exposed eye or fixate until the stimulus presentation was over. Subjects pursued from both directions during each trial block. Direction of pursuit was cued by the position of the cursor.

Experiment

We conducted three experiments within a 2 dimensional grid simulating expansion and rotations with stationary, real and simulated pursuit eye movements. Human subjects were asked to either fixate a cross on the video screen or pursue a moving point. While they perform the task, a movie depicting either expansion or clockwise-counter rotations were presented on the screen for .5 seconds. The focus of the stimuli was presented in a psuedorandom position somewhere on the 2-D grid.

After the trial, the observer was asked to adjust the perceived location of a stimulus feature, for example the focus of a rotation, to align with a large probe.

The second portion repeats the task but the eye movements are simulated, again by moving the patterns across the screen at 9°/s for all conditions. Eye movements will take place along one of four paths in both the real and simulated pursuit cases. All pursuit conditions were interleaved however each optical flow pattern was done in a separate session.

If the observers response in the real eye movement condition resembles that in the stationary eye movement condition this would imply that the observer is using an extra-retinal signal in order to compensate for the retinal shift. If their performance instead has the simulated eye movements being more correlated with the fixed eye case, this would mean that they are not incorporating an extra-retinal signal and no compensation has occurred.

Results

Results from this first experiment indicated that observers are indeed capable of estimating the focus position when presented with rotating patterns. The first experiment was a 2 dimensional paradigm designed to see whether humans can compensate for eye movement induced displacement of foci using purely rotary stimuli and how this compensation compares with their performance using expansions. For a more meaningful comparison we defined a compensation index. This index quantifies the decrease in error between the simulated and real eye movement conditions as a

proportion of the shift needed to make the perceived focus position agree with the actual focus presented. In other words, the compensation index (CI) is as follows:

$$CI = 1 - (\text{real eye movement error})/(\text{simulated eye movement error})$$

Figure 4 shows the performance of one observer during an expansion task. The pink squares represent his performance when there was no eye movement, i.e. the fixation point was stationary. As you can see he can accurately place the focus of the expansion when his eyes are stationary. When he moves his eyes in condition two, represented by the red- for rightward and green -for leftward squares, there is a very slight shift in his response, however his judgment of the focus position is still fairly accurate. In the simulated eye movement condition there is a large shift away from his true heading. He is not compensating for the apparent focus shift on his retina.

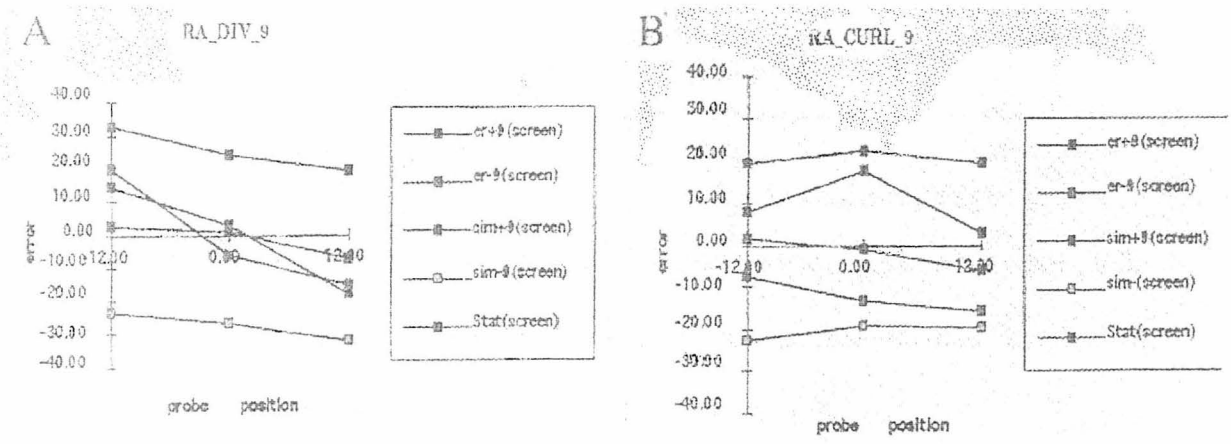
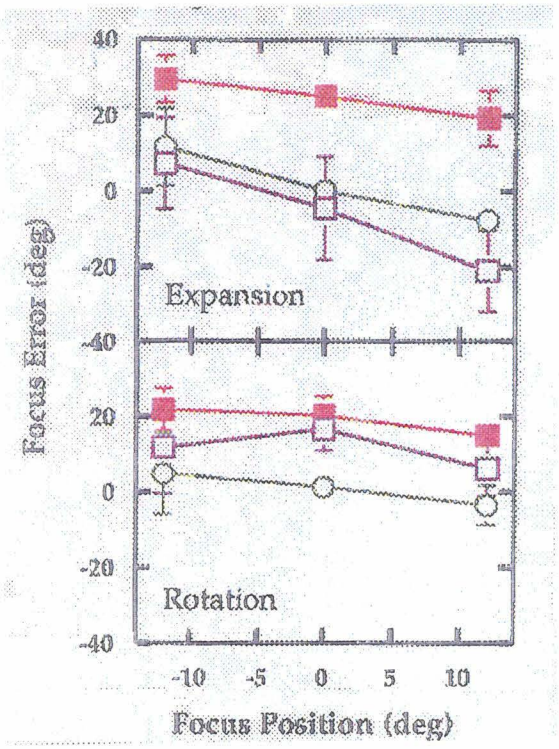


Figure 4: For both expanding (panel A) and rotating (B) motion patterns, RA's performance with real eye movements (red and green) more closely resembled that of the stationary condition. In the simulated case it is clear that no compensation is being made.

The data for our population of observers in both the expansion and rotation conditions are summarized in Figure 6. When we calculated the extent to which our brains take into account the fact that we have moved our eyes we see that the difference between the expansion and rotation case is quite striking. In the expansion case observers were compensating for their eye movements by 130%. In the rotation case the average compensation was a mere 40%. Although this

The following figure represents data averaged across four subjects (figure 5). For simplicity only rightward pursuits are shown. The blue squares represent eye pursuit, the red simulated pursuits and the green circles are the stationary eye condition. When the focus position is graphed against the judgment errors for the group we see again that the simulated eye movement condition is shifted away from the stationary case. The rotation condition had similar results as seen in this figure. Again the human brain seems to register the eye movement and effectively corrects for this gaze shift.



overcompensation was arrived at because some observers were fully compensating while others dramatically overcompensated, the smallest amount of compensation in the expansion case was 90%, in the rotation case 39%. This was interesting because the previous physiology experiment did not give a hint that there was any significant difference between the compensation in rotation cells versus

expansion cells. Indeed, there was little variation in the focus tuning shifts for expansion (18°± 3°) contraction (15°± 3°), and rotation cells (17°±4°).

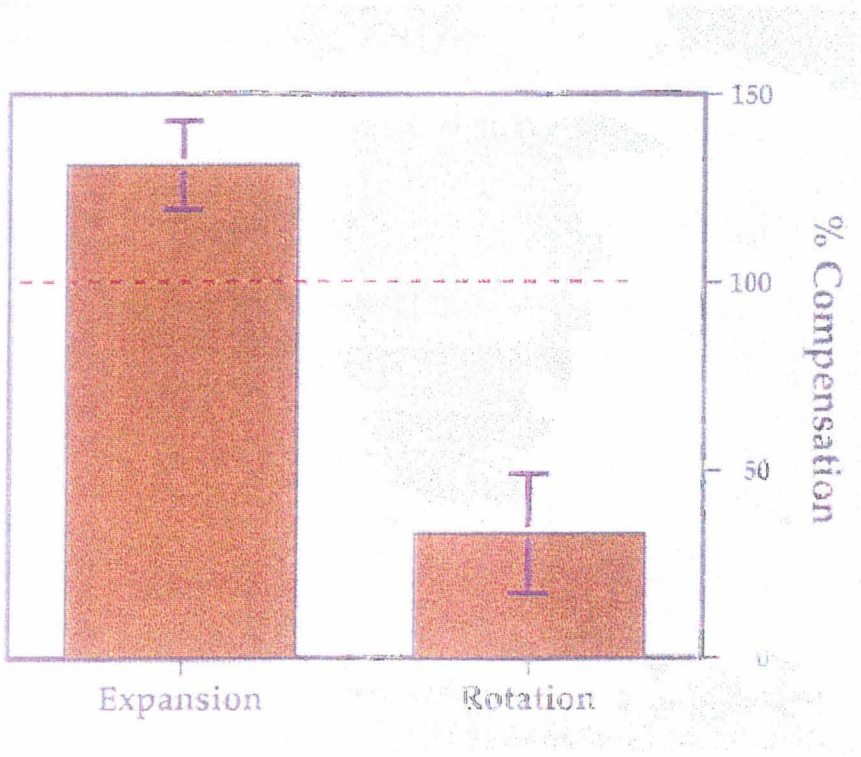


Figure 6: While subjects in both experiments compensated for eye movement induced shifts, there was a striking difference between the compensation indices for expanding and rotating patterns. The most dramatic can be seen when comparing the pre-QUEST trials. Average compensation for expanding foci was ~130% while that for rotating foci was a mere ~40%. Averaging across subjects and paradigms yielded ~105% for expansions and 42% for rotations.

In order to eliminate this high inter observer variability we implemented a variant of the QUEST maximum-likely hood estimator.[131] Here observers followed the same paradigm detailed above, however, at the end of each stimulus presentation a cross appeared superimposed on the fixation point (figure 6). This cross served to divide the screen into four quadrants. Observers were then instructed to indicate which of the four areas included the focus of the expansion or rotation. With in a trial , the focus position was varied with the 2-D QUEST method to find the true focus location

for which the apparent focus location was at the fixation point. Again performance was quite accurate in the stationary and moving eye trials while observers still made large errors during the simulated conditions.

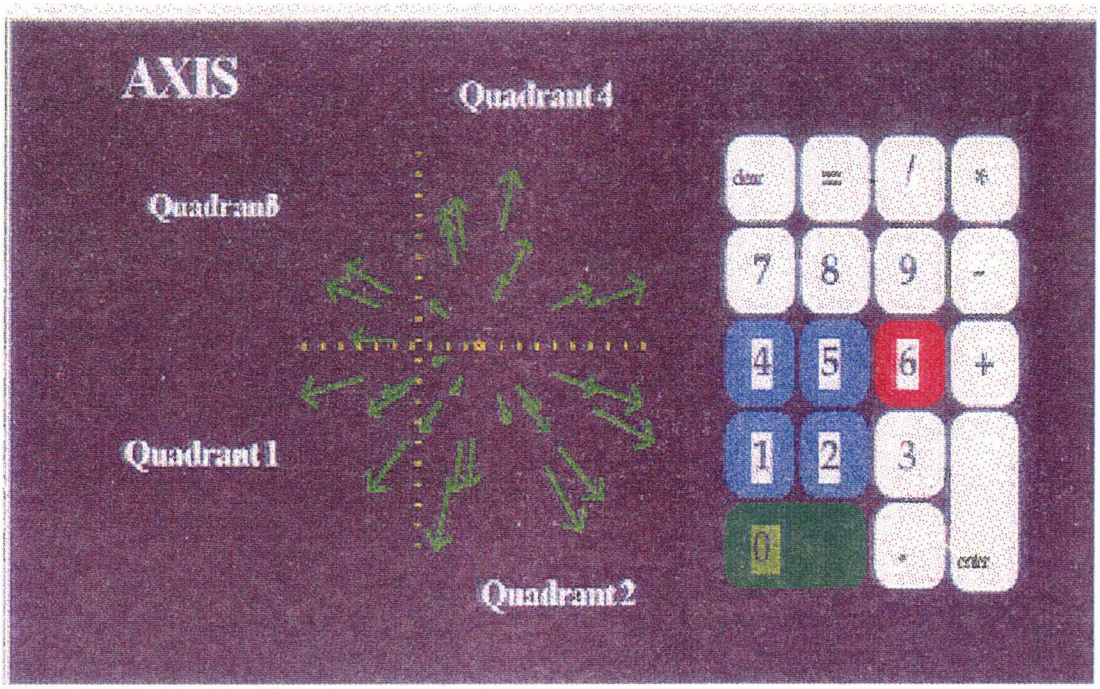


Figure 7: After the run, a quadrant appears. Subjects were instructed to identify which quadrant included the foci. If it appeared to fall on an axis, they were instructed to make their best guess.

Discussion

While humans do compensate for eye movements the extent to which they compensate does not agree with the physiology. Physiologically, expansion and rotation neurons have statistically indistinguishable responses to eye movements.

Moreover, MSTd neurons exhibited moderate compensation, on average 15° or 50% for all optic flow stimuli. In humans the extent of gaze-shift compensation during rotations agrees well with the physiological prediction. However humans fully compensate when presented with expanding stimuli, a 100% improvement over the neurons.

What these results could indicate is that expanding and rotating motion stimuli could be processed in separate perceptual channels in humans. This idea is not a new one and is supported by the findings of Geesaman and Qian in their 1996 paper reporting novel speed illusions involving expansion and rotation patterns. In that paper they used random dot stimuli that was controlled for dot speed. They found that the moving features in expanding patterns appeared to move faster than those in rotating patterns. This apparent increased speed was modulated by the strength of the global motion signal. This result was not dependent on a specific retinal stimulus location.[132] Similarly it has been noted that observers in MRI experiments also have responses contrary to responses reported by physiology when exposed to the same expansion and contraction stimuli (personal communication with R. Tootell). This lends support to the idea that optic flow stimuli are processed independently in the brain.

That the observers only partially compensate in the rotation condition could also support the notion that the role of the rotation cells in MSTd may be utilized for entirely different processes for example image stabilization and not heading. Although we did not find differences in the focus tuning of MSTd neurons tuned to varying optic flow stimuli, our population was biased by expansion cells. The literature reports a

ratio of approximately 3:1 expansions over rotations. The literature also abounds with reports that MSTd cells are preferentially selective for radially expanding patterns or spirals that are largely radial. One argument could be that expansion cells are more abundant in MSTd because they are more important for self motion. As we continue with this project and explore human and neuronal psychophysical responses to a wider range of optic flow stimuli in a variety of conditions hopefully some light will be shed on this perceptual processing issue.

Conclusion

The present study introduces the novel idea that humans like MSTd neurons can compensate for the effects of gaze shifts using rotating motion stimuli. More importantly the extent of these gaze shifts also seem to be dependent on an extra-retinal signal. While these points are shared by the psychophysical and physiological paradigms, there are some unexplained differences between human performance and that of the neurons. Humans fully compensate for eye movement effects when presented with expanding stimuli but only partially compensate with rotations. This is not to discount the importance of the rotary stimuli. While the computed compensation index was less than that found for expanding stimuli, they were in better agreement with the MSTd population response. This would suggest that it is not possible to make simple comparisons between human psychophysical performance and physiological behavior.

CHAPTER 7:
CONCLUSION

7

It may not be surprising that a book published 47 years ago could have as much influence on contemporary research in motion processing as Gibson's *Perception of the Visual World*. What is surprising is that it was practically forgotten until the mid 1970's, although it tackled then major questions in motion research. James Gibson's early views on how we are able guide our movements using optic flow alone has recently resulted in a cascade of scientific efforts ironically first in robot vision, then psychophysical research and now neurophysiological ones.

This thesis brings Gibson's proposal back to the brain. We started with insights gained from computational models which led to more concrete understandings of the problem of navigation. In these studies we found that the necessary elements needed for obtaining accurate estimates of heading are flow field noise, depth variations in the flow field, and the number of elements in the flow field. It took the human perception experiments to show us that humans can accurately judge our heading based solely on optical flow. However, it was also through psychophysics that the debate which began in the mathematical literature whether the process was purely retinal or extra-retinal in nature was partially solved. Extra-retinal signals are vital in order for

biological observers to accomplish the heading task as conditions deteriorate due to lack of depth variations in the stimulus, noisy conditions, or under high rotational eye velocities. These results suggested that retinal and extra-retinal mechanisms may work together in the primate visual system to enable observers to accurately estimate their heading in natural environments. The neurophysiological contribution was to point to the area in the primate brain where this deduction could be taking place. Their candidate- MSTd. A fairly strong case has been made that MSTd processes optic flow. Area MSTd has extra-retinal smooth pursuit signals that are independent of visual input, its responses depend on the global motion pattern in the scene, and it has a receptive field large enough to encompass a large fraction of the flow field.

By directly measuring MSTd neurons responses to optic flow fields in the presence of pursuit eye movements we added the next link. We found that not only are many MSTd neurons tuned to the position of the focus in an optic flow pattern (e.g. expansion, contraction and rotation), in addition, many shift their retinal focus tuning during eye movement in the same direction as the shift in the retinal focus induced by that movement. This focus tuning shift can only be attributed to an eye-movement signal to MSTd, because an identical retinal stimulus in the absence of eye movement produced no such shift.

In performing this experiment we also took Gibson's original idea a step further. In the study of self motion, the expansion stimulus, that which corresponds to the optic flow associated with forward motion, had been given the most attention while the other optic flow patterns had been largely ignored. While their exact purposes have

yet to be worked out, our experiment found that all classes of neurons exhibited a shift. This generated the need for another study to see whether human observers had similar perceptual responses to rotation patterns as they did for expanding ones. This introduced the novel idea that humans, like MSTd neurons, can also compensate for the effects of gaze shifts using rotating motion stimuli. Maybe more importantly we find that while the psychophysical and physiological paradigms are similar in their responses, there are some unexplained differences between human performance and that of the neurons. This suggests to us that it is not possible to make simple comparisons between human psychophysical performances and physiological behavior.

The question of how we navigate in the world is by no means solved. Although we found more evidence that MSTd is central to the computation of heading in the brain and gained some comparative insights as to how humans perceive various motion patterns, it is highly likely that MSTd is not working alone and that we have yet to determine the true role of rotation neurons. On the neurophysiological front there is still much work to be done to determine how the three classes of neurons found in MSTd are organized. Is it a hierarchy with retinal neurons strategically grouped to channel information to the shifting world neurons? Does MSTd merely gather the information and another area pools the responses from clusters of MSTd nodes to form an impression of heading in the world? On the psychophysical side how do the rotation, contraction, or spiral cells fit into this scheme? Does their presence indicate a more general phenomenon of perceptual stability in the face of retinal motion due to smooth pursuit eye movements? Or are they too a part of the navigation network?

To answer these questions a logical next step would be to return to electrophysiology armed with the knowledge gained from psychophysics and find out how the macaque perceives the expanding and rotating motion patterns. One major drawback with the electrophysiology was that our behavioral task was a relatively passive one. The monkey was trained to fixate and pursue only. We don't know how *his* perceptions are related to the activity recorded in his brain. This can be solved in two complimentary ways. 1. We can repeat the procedures but train the monkey to report where he thinks the foci of the various motion patterns lie. 2. We can see how these heading judgments are influenced if we microstimulate neurons in MSTd. Another possible avenue would be to use imaging techniques to see the brain in action as a monkey or human performs these tasks. Then it would be more clear whether MSTd is acting alone or in concert with a few other areas.

Gibson's work may have collected a lot of dust in the years following its publication, but it has finally come to be seen as a valuable cornerstone in the field of self motion. His work merged the seemingly unrelated worlds of physics and perception in an elegantly simple idea: our perception of where we are going is based on the focus of an expanding 2-D array of light on our retinas. The avalanche of new experiments and the resulting information almost ensures that we will soon know whether his theory is true or false.

BIBLIOGRAPHY

[1] Warren, WH (1995). Chapter 8. Self-Motion: Visual Perception and Visual Control.. In : *Perception of Space and Motion.* 1995. Academic Press

[2] Gibson, JJ (1950). The Perception of the Visual World. Houghton Mifflin, Boston.

[3] Helmholtz,H. von (1925). handbook on physiological optics (3rd edition,JPC Southall, Trans.). New York:Dover. (Original work published in 1867)

[4] Gibson, JJ, Olum, P.,and Rosenblatt, F. (1955). Parallax and persspective during aircraft landings. Am. J. Psychol. **68**, 372-385.

[5] Whittaker,E. (1904). A Treatise on the Analytical Dynamics of Particles and Rigid Bodies (reprinted in 1944). Dover , NY

[6] Longuet-Higgins,HC, andPrazdny,K. The interpretation of a moving retinal image. Proc. Ro. Soc. of London, B, 208, 385 -397. and Warren (1995) sited above.

[7] adapted from Longuet-Higgins,HC, andPrazdny,K. The interpretation of a moving retinal image. Proc. Ro. Soc. of London, B, 208, 385 -397. and Warren (1995) sited above.

[8] Longuet-Higgins,HC, andPrazdny,K. The interpretation of a moving retinal image. Proc. Ro. Soc. of London, B, 208, 385 -397. and Warren (1995) sited above.

[9] Longuet-Higgins,HC, andPrazdny,K. The interpretation of a moving retinal image. Proc. Ro. Soc. of London, B, 208, 385 -397.

[10] Perrone, JA (1992). Model for the computation of self-motion in biological systems. Journal of the Optical Society of America A, 9, 177-194.

[11] Prazdny, K (1980). Egomotion and relative depth map from optic flow. Biological Cybernetics, 36, 87-102.

[12] van den Berg, AV (1992). robustness of perception of heading from optic flow. Vision research, 32, 1285-1296.

[13] Gibson, JJ, Olum, P.,and Rosenblatt, F. (1955). Parallax and persspective during aircraft landings. Am. J. Psychol. **68**, 372-385.

[14] Lee, DN. (1974). Visual information during locomotion.. In: *Perception: Essays in Honor of James J. Gibson*, RB Macleod and HL Pick (Eds.). Cornell University Press, New York, pp. 250 -267.

[15] Koenderink, JJ and Doorn, AJ van (1976). Local structure of movement parallax of the plane. J. Opt. Soc Am. 66, 717-723.

[16] Koenderink, JJ and Doorn, AJ van (1981). Exterospecific component of the motion parallax field. J. Opt. Soc Am. 71, 953-957.

[17] Cutting,JE, Springer, K, Braren, PA, and Johnson, SH, (1992). Wayfinding on foot from information in retinal, not optic, flow. Journal of Experimental Psychology: General, 121, 41 - 72.

[18] Longuet-Higgins,HC, andPrazdny,K. (1980). The interpretation of a moving retinal image. Proc. Ro. Soc. of London, B, 208, 385 -397.

[19] Ullman,S (1979). The interpretation of visual motion. Cambridge, Mass: MIT Press.

[20] Prazdny,K (1980). Egomotion and relative Depth map from optical flow. Biological Cybernetics, 36, 87-102.

[21] Tsai,RY, and Huang, TS (1984a). Estimating three-dimensional motion parameters of a rigid planar patch:III. Finite point correspondences and three-view problem. IEEE Transactions on Acoustic Speech Signal Processing. ASSP-32, 213-220.

[22] Tsai,RY, and Huang, TS (1984b). Uniqueness and estimation of three-dimansional motion parameters of rigid objects with curved surfaces. IEEE Transactions on Pattern Analysis and Machine Intelligence, PAM-6, 13-27.

[23] Bruss,AR and Horn,BKP(1983).Passive navigation. Computer Vision, Graphics, and Image Processing,21,3-20.

[24] Heeger, DJ and Jepson,AD (1992). Subspace methods for recovering rigid motion. I: Algorithm and implementation. International Journal of Computer Vision.7, 95-117.

[25] Lawton,DT.(1983). Processing translation motion sequences. Computer Vision, Graphics, and Image Processing, 22,116-144.

[26] Prazdny ,K.(1981). Determining the instantaneous direction of motion from optic flow. Computer Vision, Graphics, and Image Processing,17,238-258.

[27] Hatsopoulos,NG and Warren,WH (1991). Visual navigation with a neural network. Neural Networks, 4,303-317.

[28] Koenderink, JJ and Doorn, AJ van (1981). Exsterospecific component of the motion parallax field. J. Opt. Soc Am. 71, 953-957.

[29] Regan,D.(1986). Visual processing of four kinds of relative motion. Vision research 26:127-145.

[30] Longuet-Higgins,HC and Prazdny,K (1980) The interpretation of a moving retinal image, Proc. R. Soc. London Ser. B 208,385-397.

[31] Reiger, JH and Lawton, DT (1985) Processing differential image motion", J. Opt Soc. Am. A2, 354-360.

[32] Verri,A, Girosi,F, and Torre, V. (1989). Mathematical properties of the two dimensional motion field: from singular points to motion parameters. J. Opt. Soc. AM. A6, 698-712.

[33] Richards,W (1975). "Visual space perception," in Handbook of Perception, EC Carterette and MP Friedman, eds. (Academic New York), Vol 5, pp. 351-386.

[34] Regan,D, (1985).Visual flow and the direction of locomotion." Science 277, 1064-1065.

[35] Matin, L. (1982). Visual localization and eye movements. In WA Wagenaar, AH Wertheim, and HW Leibowitz (Eds), Tutorials on motion perception (pp 101-156). New York:Plenum.

[36] von Holst, E. (1954). Relations between the centeral nervous system and the peripheral organs. Animal Behavior. 2, 89-94.

[37] Hansen,R(1979). Spatial localization during pursuit eye movements. Vision Research. 19,1213-1221.

[38] Cutting,JE, Springer, K, Braren, PA, and Johnson, SH, (1992). Wayfinding on foot from information in retinal, not optic, flow. Journal of Experimental Psychology: General, 121, 41 - 72.

[39] Gibson, JJ (1950). The Perception of the Visual World. Houghton Mifflin, Boston.

[40] Gibson (1966). The senses considered as perceptual sysytems. Botson: Houghton Mifflin

[41] Wood,RW (1895) The haunted swing illusion. Psychological Review 2:277-278.

[42] Werkhoven,P, Koenderink JJ (1991) Visual processing of rotary motion. Perct Psychophys 49:73-82.

[43] Johnston,IR, White, GR, and Cumming, RW (1973). The role of optical expansion patterns in locomotor control. American Journal of Psychology, 86, 311 -324.

[44] Llewellyn, KR (1971). Visual guidance of locomotion. Journal of Experimental Psychology, 91, 224-230.

[45] Cutting,JE, Springer, K, Braren, PA, and Johnson, SH, (1992). Wayfinding on foot from information in retinal, not optic, flow. Journal of Experimental Psychology: General, 121, 41 - 72.

[46] Warren,WB; Morris,M; Kalish, M.(1988). Perception of translational heading from optic flow. Journal of Experimental Psychology:Human Perception and Performance. 14(4):646-660.

[47] warren 91

[48] Warren,WB; Morris,M; Kalish, M.(1988). Perception of translational heading from optic flow. Journal of Experimental Psychology:Human Perception and Performance. 14(4):646-660.

[49] warren 89

[50] Blackwell 88

[51] Drury and Andersen 1995

[52] Poggio,T; Verri,A:Torre,V.(1991). Green Theorems and Qualitative Properties of the Optical Flow. Manuscript.

[53] Koenderink, JJ and Doorn, AJ van (1981). Exsterospecific component of the motion parallax field. J. Opt. Soc Am. 71, 953-957.

[54] Keonderink,JJ; van Doorn, AJ.(1987). Facts on optic flow. Biol. Cybern. 56(4):247-54.

[55] Longuet-Higgins,HC and Prazdny,K (1980) The interpretation of a moving retinal image, Proc. R. Soc. London Ser. B 208,385-397.

[56] Tsai,RY, and Huang, TS (1984a). Estimating three-dimensional motion parameters of a rigid planar patch:III. Finite point correspondences and three-view problem. IEEE Transactions on Acoustic Speech Signal Processing. ASSP-32, 213-220.

[57] Reiger,JH; Lawton, DT.(1985). Processing of differential image motion. Journal of the Optical Society of America. 2(2):354-359.

[58] Longuet-Higgins,HC and Prazdny,K (1980) The interpretation of a moving retinal image, Proc. R. Soc. London Ser. B 208,385-397.

[59] Cutting 86

[60] Reiger,JH and Toet,L (1985). Human visual navigation in the presence of 3D rotations. Biological Cybernetics. 52, 377-381.

[61] van den Berg, Av (1992). Robustness of perception of heading from optic flow. Vision research 32, 1285-1296.

[62] van den Berg, AV (1993). Perception of heading. nature, 365, 497-498.

[63] van den Berg, AV and Brenner,E (1993). Humans combine the optic flow with static depth cues for robust perception of headng. Vision Research. Vol 34, 16, 2153-2167.

[64] Mack,A and Herman,E (1973). Position constancy during pursuit eye movement. An investigation of the Filehne illusion. Quartery Journal of Experimental Psychology. 25, 71-84.

[65] Mack,A and Herman,E (1978). Loss of position constancy during pursuit eye movements. Vision research. 18, 55-62.

[66] Matin,L (1982). Visual localization and eye movements. In Wertheim,AH, Wagenaar,WA and Leibowitz,HW (Eds). utorials on motion perception. New York: Plenum Press.

[67]Saito, H; Yukie,M;Tanaka,K;Hikosaka,K;Fukada,Y;Iwai,E. Integration of Direction Signals of Image Motion in the Superior Temporal Sulcus of the Macaque Monkey. Journal of Neuwoscience. 1986 Jan; 6(1): 145-157.

[68] Desimone,R; Ungerlieder,L. Multiple Visual Areas in the Caudal Superior Temporal Sulcus of the Macaque. The Journal of Comparative Neurology. 1986; 248: 164-189.

[69] Boussaoud,D.;Ungerlieder,L;Desimone,R. Pathways for Motion Analysis: Cortical Connections of the Medial Superior Temporal and Fundus of the Superior Temporal Visual Areas in the Macaque. Journal of Comparative Neurology. 1990: 296:462-495.

[70] Maioli,M; Squartrito,S;Domeniconi,R. Projections from the visual cortical areas of the superior temporal sulcus to the lateral terminal nucleus of the accessory optic system in macaque monkeys. Brain Research. 1989; 498:389-392.

[71] Desimone,R; Ungerlieder,L. Multiple Visual Areas in the Caudal Superior Temporal Sulcus of the Macaque. The Journal of Comparative Neurology. 1986; 248: 164-189.

[72]Simpson,J; Leonard, C; Soodak, R. The accessory optic system. Analyzer of self motion. Ann N Y Acad Sci. 1988; 545:170-9.

[73]Boussaoud,D.;Ungerlieder,L;Desimone,R. Pathways for Motion Analysis: Cortical Connections of the Medial Superior Temporal and Fundus of the Superior Temporal Visual Areas in the Macaque. Journal of Comparative Neurology. 1990: 296:462-495.

[74] Gibson, J. What gives rise to the perception of motion? Psychological Review. 1968; 75(4): 347-352.

[75] Boussaoud,D.;Ungerlieder,L;Desimone,R. Pathways for Motion Analysis: Cortical Connections of the Medial Superior Temporal and Fundus of the Superior Temporal Visual Areas in the Macaque. Journal of Comparative Neurology. 1990: 296:462-495.

[76] Zeki,S. 1978 a Functional organization of a visual area in the posterior bank of the superior temporal sulcus of the rhesus monkey. J. Physiol., London. 236,549-573.

[77] Zeki,S. 1978 b Cells responding to changing image size and disparity in the cortex of the rhesus monkey. J. Physiol., London. 242, 827-841.

[78] Albright,T;Desimone,R;Gross,C. Columnar Organization of Directionally Selective Cells in Visual Area MT of the Macaque. Journal of Neurophysiology. 1984 Jan; 51(1): 16-31.

[79] Wurtz,R; Komatsu,H. Relation of cortical area MT and MST to pursuit eye movements. I. Localization and visual properties of neurons. Journal of Neurophysiology. 1988 Aug; 60(2): 580 -603.

[80] Newsome,W;Wurtz,R;Komatsu,H. Relation of Cortical Areas MT and MST to pursuit eye movements. II. Differentiation of retinal from extraretinal inputs. Journal of Neurophysiology. 1988 Aug: 60(2): 604-620.

[81] Komatsu,H;Wurtz,R. Relation of Cortical Areas MT and MST to pursuit eye movements. III. Interaction with full-field visual stimulation. Journal of Neurophysiology. 1988 Aug. 60(2):621-644.

[82] Tanaka,K; Sugita,Y; Moriya,M;Saito,H.Analysis of Object Motion in the Ventral Part of the Medial Superior Temporal Area of the Macaque Visual Cortex. Journal of Neurophysiology. 1993 Jan; 69(1): 128-142.

[83] Saito, H; Yukie,M;Tanaka,K;Hikosaka,K;Fukada,Y;Iwai,E. Integration of Direction Signals of Image Motion in the Superior Temporal Sulcus of the Macaque Monkey. Journal of Neuwoscience. 1986 Jan; 6(1): 145-157.

[84] Komatsu,H;Wurtz,R. Relation of Cortical Areas MT and MST to pursuit eye movements. III. Interaction with full-field visual stimulation. Journal of Neurophysiology. 1988 Aug. 60(2):621-644.

[85] Roy, J-P; Wurtz,R. The role of disparity-sensitive cortical neurons in signalling the direction of self-motion. Nature. 1990 Nov 8; 348: 160-163.

[86] Newsome,W;Wurtz,R;Komatsu,H. Relation of Cortical Areas MT and MST to pursuit eye movements. II.Differentiation of retinal from extraretinal inputs. Journal of Neurophysiology. 1988 Aug: 60(2): 604-620.

[87] Wurtz,R; Komatsu,H. Relation of cortical area MT and MST to pursuit eye movements. I. Localization and visual properties of neurons. Journal of Neurophysiology. 1988 Aug; 60(2): 580 -603.

[88] Komatsu,H;Wurtz,R. Relation of Cortical Areas MT and MST to pursuit eye movements. III. Interaction with full-field visual stimulation. Journal of Neurophysiology. 1988 Aug. 60(2):621-644.

[89] Tanaka,K; Sugita,Y; Moriya,M;Saito,H.Analysis of Object Motion in the Ventral Part of the Medial Superior Temporal Area of the Macaque Visual Cortex. Journal of Neurophysiology. 1993 Jan; 69(1): 128-142.

[90] Tanaka,K;Saito,H. Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the Macaque monkey. Journal of Neurophysiology. 1989 Sep; 62(3): 626-641.

40. Orban,G; Lagae,L;Verri,A;Raiguel,S; Xiao,D; Maes,H;Torre,V. First-Order analysis of optic flow in monkey brain. Proceedings of the National Academy of Science. 1992 Apr; 89: 2595-2599.

41. Graziano,M;Andersen,R;Snowden,R. Tuning of MST neurons to spiral motions. Journal of Neuroscience. 1994 Jan; 14(1):54-67.

42. Duffy,C;Wurtz,R. Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. Journal of Neurophysiology. 1991 Jun; 65(6): 1329-1345.

43. Duffy,C;Wurtz,R. Sensitivity of MST neurons to optic flow stimuli. II. Mechanisms of response selectivity revealed by small-field stimuli. Journal of Neurophysiology. 1991 Jun; 65(6): 1346-1359

44. Graziano,M;Andersen,R;Snowden,R. Tuning of MST neurons to spiral motions. Journal of Neuroscience. 1994 Jan; 14(1):54-67.

45. Tanaka,K;Saito,H. Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the Macaque monkey. Journal of Neurophysiology. 1989 Sep; 62(3): 626-641.

[91] Tanaka,K; Fukada,Y;Saito,H. Underlying Mechanisms of the Response Specificity of Expansion/Contraction and Rotation Cells in the Dorsal Part of the Medial Superior Temporal Area of the Macaque Monkey. Journal of Neuroscience. 1986; 6(1): 134-144.

[92] Orban,G; Lagae,L;Verri,A;Raiguel,S; Xiao,D; Maes,H;Torre,V. First-Order analysis of optic flow in monkey brain. Proceedings of the National Academy of Science. 1992 Apr; 89: 2595-2599.

[93] Komatsu,H;Wurtz,R. Relation of Cortical Areas MT and MST to pursuit eye movements. III. Interaction with full-field visual stimulation. Journal of Neurophysiology. 1988 Aug. 60(2):621-644.

[94] Tanaka,K; Fukada,Y;Saito,H. Underlying Mechanisms of the Response Specificity of Expansion/Contraction and Rotation Cells in the Dorsal Part of the Medial Superior Temporal Area of the Macaque Monkey. Journal of Neuroscience. 1986; 6(1): 134-144.

[95] Duffy,C;Wurtz,R. Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. Journal of Neurophysiology. 1991 Jun; 65(6): 1329-1345.

[96] Duffy,C;Wurtz,R. Sensitivity of MST neurons to optic flow stimuli. II. Mechanisms of response selectivity revealed by small-field stimuli. Journal of Neurophysiology. 1991 Jun; 65(6): 1346-1359.

[97] Graziano,M;Andersen,R;Snowden,R. Tuning of MST neurons to spiral motions. Journal of Neuroscience. 1994 Jan; 14(1):54-67.

[98] Orban,G; Lagae,L;Verri,A;Raiguel,S; Xiao,D; Maes,H;Torre,V. First-Order analysis of optic flow in monkey brain. Proceedings of the National Academy of Science. 1992 Apr; 89: 2595-2599.

[99] Tanaka,K; Fukada,Y;Saito,H. Underlying Mechanisms of the Response Specificity of Expansion/Contraction and Rotation Cells in the Dorsal Part of the Medial Superior Temporal Area of the Macaque Monkey. Journal of Neuroscience. 1986; 6(1): 134-144.

[100] Duffy,C;Wurtz,R. Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. Journal of Neurophysiology. 1991 Jun; 65(6): 1329-1345.

[101] Duffy,C;Wurtz,R. Sensitivity of MST neurons to optic flow stimuli. II. Mechanisms of response selectivity revealed by small-field stimuli. Journal of Neurophysiology. 1991 Jun; 65(6): 1346-1359

[102] Tanaka,K; Fukada,Y;Saito,H. Underlying Mechanisms of the Response Specificity of Expansion/Contraction and Rotation Cells in the Dorsal Part of the Medial Superior Temporal Area of the Macaque Monkey. Journal of Neuroscience. 1986; 6(1): 134-144.

[103] Graziano,M;Andersen,R;Snowden,R. Tuning of MST neurons to spiral motions. Journal of Neuroscience. 1994 Jan; 14(1):54-67.

[104] Graziano,M;Andersen,R;Snowden,R. Tuning of MST neurons to spiral motions. Journal of Neuroscience. 1994 Jan; 14(1):54-67.

[105] Tanaka,K;Saito,H. Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the Macaque monkey. Journal of Neurophysiology. 1989 Sep; 62(3): 626-641.

[106] Orban,G; Lagae,L;Verri,A;Raiguel,S; Xiao,D; Maes,H;Torre,V. First-Order analysis of optic flow in monkey brain. Proceedings of the National Academy of Science. 1992 Apr; 89: 2595-2599.

[107] Komatsu,H;Wurtz,R. Relation of Cortical Areas MT and MST to pursuit eye movements. III. Interaction with full-field visual stimulation. Journal of Neurophysiology. 1988 Aug. 60(2):621-644.

[108] Tanaka,K; Fukada,Y;Saito,H. Underlying Mechanisms of the Response Specificity of Expansion/Contraction and Rotation Cells in the Dorsal Part of the Medial Superior Temporal Area of the Macaque Monkey. Journal of Neuroscience. 1986; 6(1): 134-144.

[109] Duffy,C;Wurtz,R. Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. Journal of Neurophysiology. 1991 Jun; 65(6): 1329-1345.

[110] Duffy,C;Wurtz,R. Sensitivity of MST neurons to optic flow stimuli. II. Mechanisms of response selectivity revealed by small-field stimuli. Journal of Neurophysiology. 1991 Jun; 65(6): 1346-1359.

[111] Graziano,M;Andersen,R;Snowden,R. Tuning of MST neurons to spiral motions. Journal of Neuroscience. 1994 Jan; 14(1):54-67.

[112] Orban,G; Lagae,L;Verri,A;Raiguel,S; Xiao,D; Maes,H;Torre,V. First-Order analysis of optic flow in monkey brain. Proceedings of the National Academy of Science. 1992 Apr; 89: 2595-2599.

[113] Regan,D. (1981). Visual processing of four kinds of relative motion. Vision research. 26(1):127-45.

[114]Gibson, JJ (1950). The Perception of the Visual World. Houghton Mifflin, Boston Warren,WH, and Hannon,DJ (1988). Direction of self- motion is perceived from optical flow. Nature, 336, 162-163.

[115] Warren,WH, and Hannon,DJ (1988). Direction of self- motion is perceived from optical flow. Nature, 336, 162-163.

[116] Royden,C; Banks,M;Crowell,J. The perception of heading during eye movements. Nature 360,583-585. 1992.

[117] Saito,H;Yukie,M;Tanaka,K;Hikosaka,K;Fukada,Y;Iwai,E. Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. Journal of Neuroscience. 6. 145-157. 1986

[118] Graziano,M;Andersen,R;Snowden,R. Tuning of MST neurons to spiral motions. Journal of Neuroscience. 1994 Jan; 14(1):54-67.

[119] Komatsu,H;Wurtz,R. Relation of Cortical Areas MT and MST to pursuit eye movements. III. Interaction with full-field visual stimulation. Journal of Neurophysiology. 1988 Aug. 60(2):621-644.

[120] Duffy and Wurtz 1995

[121] Judge et al Vision Re, 20

[122] Longuet-Higgins,HC and Prazdny,K (1980) The interpretation of a moving retinal image, Proc. R. Soc. London Ser. B 208,385-397.

[123] Warren, WH (1995). Chapter 8. Self-Motion: Visual Perception and Visual Control. In : Perception of Space and Motion. 1995. Academic Press

[124] Mack,A and Herman,E.(1978).Vision Research.18,55.

[125] Freeman,TCA, Crowell,JA, and Banks,MS. (1996). Investigative Opthalmology and Visual Science.37,S454.

[126] Gibson, J. What gives rise to the perception of motion? Psychological Review. 1968; 75(4): 347-352.

[127]Koenderink, JJ and van Doorn, AJ (1976). Local structure of movement parallax of the plane. J. Opt. Soc Am. 66, 717-723.

[128] Warren,WH, and Hannon,DJ (1988). Direction of self- motion is perceived from optical flow. Nature, 336, 162-163.

[129] DC Bradley, MA Maxwell, RA Andersen, MS Banks, KV Shenoy, ***Science*** Sept 13, 1997.

[131]

[132] Geesaman,B; Qian,N. (1996).

APPENDIX A:
Spiral Space Adjust

```
% GENERAL INFO:
%
%
%       The bottom level is a function called
%       'DivCurlDisplay.m', which resides in this folder as well.
%       This is a fairly general routine for creating displays
%       consisting of expansions, curls, or spirals, combined
%       with real or simulated pursuit eye movements or full-body
%       rotations.
%
%
% SPECIFIC INFO:  This program simulates a frontoparallel wall that
%                 either approaches the observer or rotates about a Z-axis.  The
%                 FOE or center of rotation can be varied.  Spiral motions can
%                 be simulated using combinations of expansion and curl (rotation).
%                 After each presentation, the observer adjusts the perceived location of some
%                 feature of the velocity field (e.g. the center of rotation) to align with
%                 a probe ("+").
%
%                 When the display simulates approach, the simulated position is
%                 an exponential function of time, such that the translational
%                 image-plane velocity field is constant (as a function of image-plane
%                 position) over time.
%
%
% HOW TO USE: The parameters that are most likely to changed have been placed
%                       at the top of this file. Feel free to change them to your needs.
%                       Press any key to start the trial.After the trial you position the
%                       pattern by pressing the appropriate keys. For left adjustments use the
%                       '1','4', and '7' keys.          For right adjustments use the '3','6', and '9'
%                       The higher the number the greater the adjustment (e.g. '1' = small step
%                       to the left and'9' = large step to the right.  Once the stimulus feature is
%                       aligned horizontally with the probe press the ESC key to adjust vertically.
%                       To go on to the next trial enter  '4' when prompted.
%
%
% NOTE: Data will be written to a unique file name containing the
%                 observer name. This means that every run will create a new output
%                 file, and it might therefore be necessary to periodically remove
%                 old output files in order to limit the total number of files
%                 created.
%
%
```

```
%       VERSION HISTORY:
%
% MAIN PARAMETERS:
%
%       flowAngle determines type of flow: 0 = expansion/contraction,
%       90 = curl, anything in between = spiral (prototypical spiral
%       = 45 degrees).
%
%       flowGradient determines the rate at which velocity increases as you
%       go away from the focus (roughly, V = flowGradient * distance.
%       positive values denote expansion/counter-clockwise rotation.
%
%       focusXY is a 1x2 vector containing the X and Y positions of the
%       pattern focus.  The value is the tangent of the angle between
%       the focus and the corresponding origin, i.e.
%       foxusX = tan(Radians( focus X in degrees )).
%
%       eyeInHeadRot = real pursuit velocity (rate at which fixation point
%       moves).  Currently only horizontal pursuits are supported.  Positive
%       = rightward.
%
%       bodyRot = full body rotation velocity (for the acutronic chair system).
%       Horizontal only.
%
%       simRot = simulated rotation rate.
%       Horizontal only.
%

SetExptLibsPath;
SetSterHeadPath;

basePath = MatlabFolderPath;

experimentPath = cd;

disp('Adding folders to Matlab search path...');
newPath = [     [basePath ':Vestibular Chair Tools']];
path( path, newPath );
disp('Done extending search path...');

Randomize;      % Make sure that we get different random numbers
                                                        % each time we start an
experiment.

screenNum = 0;                          % Choose display screen.
```

```
frameRate = AnimationTools('GetFrameRate', screenNum);          % The frameRate is being
                                                                % measured (this takes
                                                                % about one second).

%%%%%% Observer specific data. %%%%%%

observer = 'MM';                % Name of the observer.

%%%%%% Main Expt. Parameters %%%%%%
% The following variables are manipulated independently.
% In other words, all possible combinations of the specified values
% of these variables will be presented.

rotationType = 'eye';

lifeTest = 0;
motionType = 'spiral'   %  'div' (expansion), 'curl' (rotation), or 'spiral'(spirals).
numTypes = 1;
baseFileName = [rotationType];

%flowGradients = [0.6328]/frameRate; %  This number specifies how rapidly the velocity
%flowGradients = -[0.6328]/frameRate;% vector magnitudes increase with distance from
                                                                % the focus, i.e. mag =
flowGradient * distance.
                                                                % Positive values
correspond to expansion and
                                                                % counter-clockwise
rotation, negative to the
                                                                % opposite.

if (lifeTest)
        dotLife = 1000;
else
        dotLife = 0.5;
end
%probeYs = tan(Radians(0));
probeYs = tan(Radians([-12 12]));
focusXRange = tan( Radians( 5 ) );

if (strcmp( rotationType, 'eye' )==1)
        rotRate = Radians(16)/frameRate;
```

```
%       probeXs = tan(Radians([-16 -8 0 8 16]));
        probeXs = tan(Radians([-12 12]));
%       probeXs = tan(Radians([0]));
        focusYRange = tan( Radians( 5 ) );
%       focusYRange = tan( Radians( 40 ) );
%       focusYRange = tan( Radians( 0 ) );
        foeShift = tan( Radians(30) );
        maxFocusPos = Radians(21);

        eyeInHeadRots = [-rotRate rotRate 0 0 0];
        bodyRots = [0 0 0 0 0];
        monitorRotates = 0;
        screenSize = [111 75];
        viewDist = 46;
        wallScaleFactor = 0.8;
else
        rotRate = Radians(9)/frameRate;

        probeXs = tan(Radians([-30 -20 -10 0 10 20 30]));
%       focusXs = tan(Radians([-30 -15 0 15 30]));
        focusYRange = tan( Radians( 0 ) );
        foeShift = tan( Radians(24) );
        maxFocusPos = Radians(21);

        eyeInHeadRots = [0 0 0 0 0];
        bodyRots = [-rotRate rotRate 0 0 0];
        monitorRotates = 1;
        screenSize = [32.5 28.5];
        viewDist = 32;
        wallScaleFactor = 1;
end

flowGradients = rotRate*foeShift + rotRate/foeShift;
disp(['Flow gradients = ' num2str(flowGradients*frameRate) ' /sec.']);

simRots = [0 0 -rotRate rotRate 0];
numRots = 5;

%numRepetitions = 5;
numRepetitions = 3;

z = zeros(size(simRots));
if (strcmp(motionType,'div')==1)
        flowAngle = Radians(0);
elseif (strcmp(motionType,'curl')==1)
        flowAngle = Radians(90);
```

```
else                                                    % Spiral
        flowAngle = Radians(45);
        simRotsX = simRots*cos(flowAngle);
        simRotsY = simRots*sin(flowAngle);
        eyeRotsX = eyeInHeadRots*cos(flowAngle);
        eyeRotsY = eyeInHeadRots*sin(flowAngle);
%       simRotsX = z;
%       simRotsY = simRots;
%       eyeRotsX = z;
%       eyeRotsY = eyeInHeadRots;
end


baseFileName = [baseFileName '_' motionType(1:3)];

numGradients = size( flowGradients, 2 );
numPosX = size( probeXs, 2 );
numPosY = size( probeYs, 2 );

maxNumTrials = numGradients*numPosX*numPosY*numRots*numRepetitions;

%%%%% Defines %%%%%%

% numPoints was 200 --- KVS 10/21/96
numPoints = 600;            % Select the number of dots on the screen (where will be
                                        % 'numPoints' green dots and 'numPoints' red dots.
                                        % Note that there might be a lot fewer dots visible if soft
                                        % clipping is in use.

chairAcceleration = Radians(30)/(frameRate^2);

%stimDuration = 1.000;              % Amount of time rotation will be constant
                                                        % (i.e. translation display duration).
stimDuration = 0.75;
leadDuration = 0.4;

totalDuration = leadDuration + stimDuration;

%wallScaleFactor = .5;  % Expands the wall by this factor (it starts out just
                                                        % filling the screen).  Should be
just big enough
                                                        % so that no edges of the wall ever
become visible
                                                        % during any kind of trial.
```

```
if (strcmp( rotationType, 'eye' )==1)
% Clip angles were 40 --- KVS 10/21/96
        softClipAngleY = 60;      % Total vertical angle of the soft clipping window (in degrees).
        softClipAngleX = 60;      % Total horizontal angle of the soft clipping window (in degrees)
                                                % Note that the window will follow the dot rotation.
                                                % If you want the full screen size, set
'UseSoftwareClip'
                                                % to zero below.  If you want the largest possible
                                                % dynamic window, set the angles really big &
they'll be
                                                % shrunk to fit by CheckClipAngles(), below.
else
% Clip angles were 18 --- KVS 10/21/96
        softClipAngleX = 0;
        softClipAngleY = 0;
end

softClipAngleY = Radians( softClipAngleY );
softClipAngleX = Radians( softClipAngleX );
softClipAngles = [softClipAngleX softClipAngleY];


rightMaxLumFrac   = 1;                  % Choose brightness of right eye from 0 to 1.
leftMaxLumFrac    = 0.714;              % Choose brightness of left eye from 0 to 1.
interTrialIndex = 15;                   % Choose brightness for screen shown between
                                                % trials from 0 to 15. (15 = max.).

finalChairPos = Radians( 45 );

cursorDistance = viewDist;
initCursorRange = [5 5];


%%%%% Switches. %%%%%

startMethod = 'key';        % How does observer initiate a trial?
                                                % ('mouse' or 'key').

if (strcmp( rotationType, 'eye' )==1)
        viewMode = 'mono';  % 'stereo', 'mono', 'right eye' (like mono but assumes
                                                % nose centered on screen, not eye, & right eye will
                                                % be used) and 'left eye'.
else
        if ((strcmp(observer,'RAA')==1)|(strcmp(observer,'AG')==1))
                viewMode = 'left eye'
        else
                viewMode = 'right eye'
        end
end
```

```
blankEnd = 0;      % if not 0, blanks dots at end of sequence.

fastLUT = 1;       % uses default values for luminance calibration (1)
                              % instead of reading data from files (0).

INFINITY = 1e10;

%%%%% Adjustment parameters %%%%%
initFocusX = 0;
initFocusY = 0;
scaleType = 'linear';
minStepSize = Radians(4);
stepSizeInc = 2;
upkeys = ['3' '6' '9'];                 % '3', '6', '9'
downKeys = ['1' '4' '7'];               % '1', '4', '7'
scaleUpKey = ['8'];         % up arrow
scaleDownKey = ['2'];       % down arrow
repeatKey = [];   % '5'
%doneKey = [setstr(29)];                % right arrow
%abortKey = [setstr(5)];                % help
doneKey = [];               % ESC
abortKey = [];              % 'q'
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

stimFrames = round( frameRate * stimDuration );
leadFrames = round( frameRate * leadDuration );
totalFrames = stimFrames + leadFrames;
lifeFrames = round( frameRate * dotLife );

disp(' ');

depth = ScreenTools('GetDepth');
ScreenTools('SetDepth', 8, 1);

if (~isempty( observer ) )  % If observer is set to '' (empty string), the file name is set to JUNK.mat.

	baseFileName = [observer '_' baseFileName '_' num2str(Degrees(rotRate)*frameRate)];
	pathName = [cd ':Data'];
	fileName = UniqueFileName( baseFileName, pathName )
	tempFileName = [observer '_' motionType '_' num2str(Degrees(rotRate)*frameRate) '_tmp.mat'];
else
	disp('You have not specified an observer.');
	disp('Data will be written to JUNK.mat');
	disp('(Hit any key to continue)');
	pause;
```

```
        pathName = cd;
        fileName = 'JUNK.mat';
        tempFileName = [];
end

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
%
%       Set up paramTable
%
%       This is a numTrials X numParams matrix; each row
%       contains the values of all the variable parameters
%       for that trial.
%
%       Currently, the arrangement is:
%
%       flowAngle flowGradient focusX focusY eyeRot bodyRot simRot
%
paramTable = zeros( maxNumTrials, 13 );

index = 1:numRepetitions;
disp('Constructing parameter table.');
disp('This will take a few seconds...');
c = cos( flowAngle );
s = sin( flowAngle );

for i = 1:1
        A = flowAngle;
        for j = 1:numGradients
                G = flowGradients(j);
                for k = 1:numRots
                        ERX = eyeRotsX(k);
                        ERY = eyeRotsY(k);
                        BR = bodyRots(k);
                        SRX = simRotsX(k);
                        SRY = simRotsY(k);

                        for l = 1:numPosX
                                fx = probeXs(l);

                                for m = 1:numPosY
                                        fy = probeYs(m);

                                        xRand = focusXRange*(rand(numRepetitions,1)-0.5);
                                        yRand = focusYRange*(rand(numRepetitions,1)-0.5);

                                        if (strcmp( motionType, 'div' )==1)
                                                xOffset = tan( ERX*stimFrames/2 );
```

```
                                        yOffset = 0;
                                elseif  (strcmp(motionType, 'curl' )==1)
                                        xOffset = 0;
                                        yOffset = tan( ERY*stimFrames/2 );
                                else
                                        xOffset = cos(ERX*stimFrames/2;
                                        simRotsY = sin(ERX*stimFrames/2);
                                end
                                paramLine = [A G fx fy ERX ERY BR SRX SRY 0 0 xOffset
yOffset];
                                paramLine = ones(numRepetitions,1)*paramLine;
                                paramLine = [paramLine(:,1:9) xRand yRand paramLine(:,[12
13])];

                                paramTable(index,:) = paramLine;

                                index = index + numRepetitions;

                        end
                end
        end
end

numTrials = index(1)-1;
paramTable = paramTable(1:numTrials,:);

paramIndex = (1:numTrials)';
for i = 1:3
        paramIndex = ScrambleColumns( paramIndex );
end

disp('Done constructing parameter table.');
resps = zeros( numTrials, 2 );

startTrial = 1;

numTrials = size( paramTable, 1 )
numPixels = ScreenTools ('ScreenSizes');    % Set up a fixation cross at the
numPixels = numPixels(screenNum+1,:);

if (strcmp(viewMode, 'mono')~=1)
        eyeSpacing = GetEyeSpacing( observer );    % Look up the IPD for the selected observer.
else
```

```
        eyeSpacing = 0;
end
if (any(bodyRots~=0))
        rotationOffset = GetRotationOffset( observer );
else
        rotationOffset = 0;
end

disp('After each trial, press one of the keys on the numeric keypad');
disp('to bring the response probe closer to the motion pattern focus');
disp('on the next trial.');
disp(' ');
disp('The keys in the left column will shift the probe to the left.');
disp('The "1" key will shift it left by a small step, the "7" key');
disp('by a large step, and the "4" key by an intermediate step.');
disp(' ');
disp('The keys in the right-hand column shift the probe to the right');
disp('by the same step sizes.');
disp(' ');
disp('Press any key to continue');
pause;
disp(' ');
disp('If you decide that the step sizes are too small or too large,');
disp('you can increase or decrease them using the "up arrow" and');
disp('"down arrow" keys.');
disp(' ');
disp('When you are satisfied that the probe is as close to the focus');
disp('as you can get it, hit the ESC key (upper-left corner of keyboard)');
disp(' ');
disp('If the focus appears to lie beyond an edge of the screen,');
disp('press the "q" key');
disp(' ');
disp('Hit any key to initiate each trial');
disp(' ');

disp('Hit any key now to begin');
disp(' ');
EventTools('WaitKey');

disp('Starting experiment.');

ChairInit;
ChairGo;  % pre-load the ChairGo function.

%  Load the red/green color-lookup table.
```

```
ScreenTools ('SetScreen', screenNum, 0 )
if (fastLUT==0)
        AnaglyphLUT( rightMaxLumFrac, leftMaxLumFrac, ...
                                'calRedG', 'calGreenFG' );          % Install anaglyph (red/green)
CLUT.
else
        AnaglyphLUT( rightMaxLumFrac, leftMaxLumFrac, ...
                                'red', 'green' );     % Install anaglyph (red/green) CLUT.
end

% Hide the cursor.
CursorTools ('Hide');

% Run the experiment.

trialCount = startTrial;
abort = 0;
while (trialCount <= numTrials)

        trialIndex = paramIndex(trialCount);
        probeXY = paramTable(trialIndex,[3 4])+paramTable(trialIndex,[12 13]);
        flowGradient = paramTable(trialIndex,2);
        flowAngle = paramTable(trialIndex,1);
        eyeRotX = paramTable(trialIndex,5);
        eyeRotY = paramTable(trialIndex,6);
        bodyRot = paramTable(trialIndex,7);
        simRotX = paramTable(trialIndex,8);
        simRotY = paramTable(trialIndex,9);
        simRot = sqrt(simRotX^2+simRotY^2);

        if (simRot~=0)
                focusShift = 0.5*(flowGradient - ...
                                sign(flowGradient)*sqrt(flowGradient^2 - 4*simRot^2))/simRot;
        else
                focusShift = 0;
        end
        if (strcmp(rotationType,'eye')==1)
                xMin = min([probeXY(1) probeXY(1)-focusShift]) - tan(Radians(10));
                xMax = max([probeXY(1) probeXY(1)-focusShift]) + tan(Radians(10));
        else
                xMin = min([probeXY(1) probeXY(1)-focusShift]) - tan(Radians(4));
                xMax = max([probeXY(1) probeXY(1)-focusShift]) + tan(Radians(4));
        end
        initFocusXY = [rand(1,1)*(xMax-xMin)+xMin 0] + paramTable(trialIndex,[10 11]);

        probeX = probeXY(1);
```

```
        probeY = probeXY(2);
        focusX = initFocusXY(1);
        focusY = initFocusXY(2);

        adjustX = 1;
        while (adjustX)
                [focusX,responseData] = RunAdjustment('DivCurlDisplay', ...
                                                        1, focusX, scaleType, minStepSize, ...
                                                        stepSizeInc, upkeys, downKeys, ...
                                                        scaleUpKey, scaleDownKey, repeatKey, ...
                                                        doneKey, abortKey, ...
                                                        [], focusY, flowGradient, flowAngle, ...
                                                        eyeRotX, eyeRotY, bodyRot, simRotX,
simRotY, ...
                                                        chairAcceleration, leadFrames, stimFrames,
...
                                                        frameRate, viewDist, screenNum,
numPixels, ...
                                                        screenSize, numPoints, wallScaleFactor, ...
                                                        blankEnd, softClipAngles, ...
                                                        rotationOffset, monitorRotates, viewMode,
...
                                                        eyeSpacing, startMethod, interTrialIndex, ...
                                                        lifeFrames, finalChairPos, probeX, probeY
);
%disp([trialCount trialIndex probeX])
                disp(['# ' int2str(trialCount) ' of ' int2str(numTrials)]);
                adjustX = 0;
                if (focusYRange == 0)
                        disp('Hit any key to continue');
                        EventTools('WaitKey');
                else
                        if ~isnan( probeX )
                                disp('Done adjusting X.  Adjust Y ("4"=no, "6"=yes, "q"=quit)?');
                                key = 0;
                                while ((key~='4')&(key~='6')&(key~='q'))
                                        key = EventTools('WaitKey');
                                        if ((key~='4')&(key~='6')&(key~='q'))
                                                Beep( 100, 100 );
                                        elseif (key=='4')
                                                adjustY = 0;
                                        elseif (key=='6')
                                                adjustY = 1;
                                        else
                                                adjustY = 0;
```

```
                                        abort = 1;
                                end
                        end
                end
                if (adjustY)
                        [focusY,responseData] = RunAdjustment('DivCurlDisplay', ...
                                                                2, focusY, 'linear', minStepSize, ...
                                                                stepSizeInc, upkeys, downKeys, ...
                                                                scaleUpKey, scaleDownKey,
repeatKey, ...
                                                                doneKey, abortKey, ...
                                                                focusX, [], flowGradient,
flowAngle, ...
                                                                eyeRotX, eyeRotY, bodyRot,
simRotX, simRotY, ...
                                                                chairAcceleration, leadFrames,
stimFrames, ...
                                                                frameRate, viewDist, screenNum,
numPixels, ...
                                                                screenSize, numPoints,
wallScaleFactor, ...
                                                                blankEnd, softClipAngles, ...
                                                                rotationOffset, monitorRotates,
viewMode, ...
                                                                eyeSpacing, startMethod,
interTrialIndex, ...
                                                                lifeFrames, finalChairPos, probeX,
probeY );

                        if ~isnan( probeY )
                                disp('Done adjusting Y.  Adjust X again ("4"=no, "6"=yes,
"q"=quit)?');
                                key = 0;
                                while ((key~='4')&(key~='6')&(key~='q'))
                                        key = EventTools('WaitKey');
                                        if ((key~='4')&(key~='6')&(key~='q'))
                                                Beep( 100, 100 );
                                        elseif (key=='4')
                                                adjustX = 0;
                                        elseif (key=='6')
                                                adjustX = 1;
                                        else
                                                adjustX = 0;
                                                abort = 1;
                                        end
```

There is no page A14.

```
                        end
                    end
                end
            end
        end

        resps( trialIndex, : ) = [focusX focusY];

        if (abort)
            disp('ABORTING EXPERIMENT');
            disp([int2str(trialCount) ' of ' int2str(numTrials) ' COMPLETED.']);
            disp(['SAVING PROGRAM STATE TO ' tempFileName]);
            eval(['save ' tempFileName]);
            break;
        end

        trialCount = trialCount+1;
end

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

%%%%% Clean up after animation. %%%%%

ChairGo(0.0);

ScreenTools ('ShowPage', 0)                    % The Macintosh desktop is on page zero.


        % This line prevents the following lines from crashing!!
ScreenTools ('RestoreScreen')

ScreenTools ('SetDepth', depth(1), depth(2))

CursorTools('Init');


if (~abort)
        %%%%%%%%% Save the results to a Matlab format data file %%%%%%%

        %%%% UNIT CONVERSIONS %%%%

        probeXs = Degrees(atan(probeXs));
        probeYs = Degrees(atan(probeYs));
        flowGradients = flowGradients*frameRate;
        flowAngle = Degrees(flowAngle);
```

```
rotRate = Degrees(rotRate)*frameRate;
eyeInHeadRots = Degrees(eyeInHeadRots)*frameRate;
bodyRots = Degrees(bodyRots)*frameRate;
simRots = Degrees(simRots)*frameRate;
maxFocusPos = Degrees( maxFocusPos );

paramTable(:,[3 4 10:13]) = atan(paramTable(:,[3 4 10:13]));
paramTable(:,[1 3:13]) = Degrees(paramTable(:,[1 3:13]));
paramTable(:,[2 5:9]) = paramTable(:,[2 5:9])*frameRate;

responses = Degrees(atan(resps));

softClipAngleY = Degrees( softClipAngleY );
softClipAngleX = Degrees( softClipAngleX );

FA = paramTable(:,1);
FG = paramTable(:,2);
PX = paramTable(:,3);
PY = paramTable(:,4);
ERX = paramTable(:,5);
ERY = paramTable(:,6);
BR = paramTable(:,7);
SRX = paramTable(:,8);
SRY = paramTable(:,9);

FX = responses(:,1);
FY = responses(:,2);

if (strcmp( rotationType, 'eye' )==1)
        if (strcmp(motionType, 'div')==1)
                RR = ERX;
                SR = SRX;
        elseif (strcmp(motionType, 'curl' )==1)
                RR = ERY;
                SR = SRY;
%       else
%               RR = cos*(ERY + ERX)
%               SR = sin*(SRY + SRX)
        end
        ER = RR;
else
        RR = BR;
        SR = SRX;
        ER = zeros(size(RR));
end
```

```
c1 = find( abs(RR-rotRate) < .1 );
c2 = find( abs(RR+rotRate) < .1 );
c3 = find( abs(SR-rotRate) < .1 );
c4 = find( abs(SR+rotRate) < .1 );
c5 = find( (RR==0) & (SR==0) );
% Calculate response error relative to _final_
% true focus position.
FR = SR+BR;

if (strcmp( motionType, 'div' )==1)
        FXfin = FX - 0.5*stimDuration*FR;
        FYfin = FY;
else
        FXfin = FX;
        FYfin = FY - 0.5*stimDuration*FR;
end
errXfin = PX-FXfin;
errYfin = PY-FYfin;

% Calculate response error relative to _final_
% retinal focus position.
FR = FR+ER;
a = FR ~= 0;
focusShiftX = zeros(size(FR));

if any(a)
        a = find(a);
        c = cos(Radians(FA(a)));
        focusShiftX(a) = 0.5*c.*(FG(a) - ...
                sign(FG(a)).*sqrt(FG(a).^2 - 4*Radians(FR(a)).^2))./Radians(FR(a));

end

foeShift = Degrees(atan(foeShift));

% Position of retinal focus at _end_ of trial.
% (in degrees from screen center)
%       retFocusX = Degrees(atan(tan(Radians(FXfin)) + focusShiftX));
retFocusX = FXfin + foeShift*sign(FR);
retFocusY = FYfin;
```

```
errXret = PX-retFocusX;
errYret = PY-retFocusY;

Xret = zeros( numRots, numPosX );
Yret = zeros( numRots, numPosX );
Xscr = zeros( numRots, numPosX );
Yscr = zeros( numRots, numPosX );
sigmaXret = zeros( numRots, numPosX );
sigmaYret = zeros( numRots, numPosX );
sigmaXscr = zeros( numRots, numPosX );
sigmaYscr = zeros( numRots, numPosX );

for i = 1:numRots
        theIndex = eval(['c' int2str(i)]);

        X = PX( theIndex );
        errXf = errXfin( theIndex );
        errXr = errXret( theIndex );
        Y = PY( theIndex );
        errYf = errYfin( theIndex );
        errYr = errYret( theIndex );

        for j = 1:numPosX
                theIndex = find( X==probeXs(j) );

                Xr = errXr( theIndex );
                Xs = errXf( theIndex );
                Yr = errYr( theIndex );
                Ys = errYf( theIndex );

                Xret(i,j) = mean( Xr );
                sigmaXret(i,j) = std( Xr );
                Yret(i,j) = mean( Yr );
                sigmaYret(i,j) = std( Yr );
                Xscr(i,j) = mean( Xs );
                sigmaXscr(i,j) = std( Xs );
                Yscr(i,j) = mean( Ys );
                sigmaYscr(i,j) = std( Ys );
        end
end

%%%% WRITE EVERYTHING TO FILE (yes, everything)!!! %%%%
% If there's something you _don't_ want written to file, 'clear'
% it now!

oldPath = cd;
```

```
feval('cd',pathName);
eval(['save ' fileName] );
cd(oldPath);

disp(' ');
disp(['Data written to ' fileName]);
disp(['In ' pathName]);
disp(' ');

if (exist(tempFileName)==2)
        disp(['Deleting temporary file ' tempFileName]);
        eval(['delete ' tempFileName]);
end

figure(1);
set(1,'units','normalized')
set(1,'position',[0 0 1 1]);

subplot(121);
plot( probeXs', Xscr' );
hold on;
plot( probeXs', Xscr', 'o' );
%       errorbar( probeXs'*ones(1,numRots), Xscr', Xscr'-sigmaXscr', Xscr'+sigmaXscr', 'o' );
plot( probeXs', Xret' );
hold off;
axis([-20 20 -40 40])
xlabel('Probe Position (deg)');
ylabel('error');
subplot(122);
plot( probeXs', Yscr' );
hold on;
plot( probeXs', Yscr', 'o' );
plot( probeXs', Yret' );
hold off;
axis([-20 20 -40 40])

figure(2)
set(2,'units','normalized')
set(2,'position',[0 0 1 1]);

subplot(121);
plot( eyeInHeadRots, Xscr, 'o' );
axis([-20 20 -40 40])
xlabel('Eye Pursuit Rate');
ylabel('error');
subplot(122);
```

```
        plot( simRots, Xscr, 'o' );
        axis([-20 20 -40 40])
        xlabel('Sim. Rot. Rate');
        ylabel('error');

        textName = [fileName(1:(length(fileName)-4)) '.txt'];

        t = [probeXs'];
        for i = 1:numRots
                t = [t Xscr(i,:)' sigmaXscr(i,:)'];
                t = [t Xret(i,:)' sigmaXret(i,:)'];
        end
        for i = 1:numRots
                t = [t Yscr(i,:)' sigmaYscr(i,:)'];
                t = [t Yret(i,:)' sigmaYret(i,:)'];
        end

        eval(['save ' textName ' t /ascii /tabs']);
end
```

APPENDIX B:
SPIRAL SPACE QUEST

```
% GENERAL INFO:
%
%
%       The bottom level is a function called
%       'DivCurlDisplay.m', which resides in this folder as well.
%       This is a fairly general routine for creating displays
%       consisting of expansions, curls, or spirals, combined
%       with real or simulated pursuit eye movements or full-body
%       rotations.
%
%
% SPECIFIC INFO:  This program simulates a frontoparallel wall that
%                 either approaches the observer or rotates about a Z-axis.  The
%                 FOE or center of rotation can be varied.  Spiral motions can
%                 be simulated using combinations of expansion and curl (rotation).
%                 After each presentation, the observer moves a cursor with the mouse
%                 to indicate perceived location of some feature of the velocity field
%                 (e.g. the center of rotation).
%
%                 When the display simulates approach, the simulated position is
%                 an exponential function of time, such that the translational
%                 image-plane velocity field is constant (as a function of image-plane
%                 position) over time.
%
%
% HOW TO USE: The parameters that are most likely to changed have been placed
%                       at the top of this file. Feel free to change them to your needs.
%                       Press the mouse button to start the trial.
%                       After the trial you position the cursor and press the mouse button.
%                       If you want to skip the trial you press the space bar.
%
% NOTE: Data will be written to a unique file name containing the
%                 observer name. This means that every run will create a new output
%                 file, and it might therefore be necessary to periodically remove
%                 old output files in order to limit the total number of files
%                 created.
%
%
%       VERSION HISTORY:
%
% MAIN PARAMETERS:
%
%       flowAngle determines type of flow: 0 = expansion/contraction,
%       90 = curl, anything in between = spiral (prototypical spiral
%       = 45 degrees).
%
```

```
%       flowGradient determines the rate at which velocity increases as you
%       go away from the focus (roughly, V = flowGradient * distance.
%       positive values denote expansion/counter-clockwise rotation.
%
%       focusXY is a 1x2 vector containing the X and Y positions of the
%       pattern focus. The value is the tangent of the angle between
%       the focus and the corresponding origin, i.e.
%       foxusX = tan(Radians( focus X in degrees )).
%
%       eyeInHeadRot = real pursuit velocity (rate at which fixation point
%       moves). Currently only horizontal pursuits are supported. Positive
%       = rightward.
%
%       bodyRot = full body rotation velocity (for the acutronic chair system).
%       Horizontal only.
%
%       simRot = simulated rotation rate.
%       Horizontal only.
%

SetExptLibsPath;
SetSterHeadPath;
SetEyeTrackPath;

basePath = MatlabFolderPath;

experimentPath = cd;

disp('Adding folders to Matlab search path...');
newPath = [     [basePath ':Vestibular Chair Tools']];
path( path, newPath );
disp('Done extending search path...');

Randomize;      % Make sure that we get different random numbers
                                                        % each time we start an
experiment.

screenNum = 0;                                  % Choose display screen.

frameRate = AnimationTools('GetFrameRate', screenNum);          % The frameRate is being

                                % measured (this takes

                                % about one second).

%%%%%% Observer specific data. %%%%%%
```

```
observer = ''                   % Name of the observer.

jimCall = 0;

%%%%%% Main Expt. Parameters %%%%%%
% The following variables are manipulated independently.
% In other words, all possible combinations of the specified values
% of these variables will be presented.

rotationType = 'eye';
rotType = 'real';
rotationAngle = Radians(0);

motionType = 'div'   %  'div' (expansion), 'curl' (rotation), or 'spiral'.

baseFileName = [rotationType '_' motionType(1:3)];
numRepetitions = 1;
eyeTrace = 1;

if (strcmp( rotationType, 'eye' )==1)
        rotRate = Radians(15)/frameRate;

        % probePositions specified as [x y; x y; ....] (deg)
        probePositions = tan(Radians( ...
                        [0 0]))';

        flowGradient = 0.65/frameRate;

        % Desired screen-retina focus shift
%       foeShift = Radians(30);
        if (strcmp(rotType,'real')==1)
                eyeInHeadRots = [-rotRate rotRate];
                bodyRotRates = [0 0];
                simRotRates = [0 0];
        elseif (strcmp(rotType,'sim')==1)
                eyeInHeadRots = [0 0 0];
                bodyRotRates = [0 0 0];
                simRotRates = [-rotRate rotRate 0];
        else
                eyeInHeadRots = [-rotRate rotRate 0 0 0];
                bodyRotRates = [0 0 0 0 0];
                simRotRates = [0 0 -rotRate rotRate 0];
        end
%else
%       eyeInHeadRots = [-rotRate rotRate];
%       bodyRotRates = [0 0];
%simRotRates = [0 0 -rotRate rotRate 0];
%end
```

```
        monitorRotates = 0;
        screenSize = [30.2 22.2];
        viewDist = 30;
%       viewDist = 42;
%       screenSize = [110 76];   %projector
%       viewDist = 46;
%       wallScaleFactor = 0.6;
        wallScaleFactor = 0.8;
% Clip angles were 40 --- KVS 10/21/96
        softClipAngleY = 40;      % Total vertical angle of the soft clipping window (in degrees).
        softClipAngleX = 40;      % Total horizontal angle of the soft clipping window (in degrees)
                                  % Note that the window will follow the dot rotation.
                                  % If you want the full screen size, set
'UseSoftwareClip'
                                  % to zero below.  If you want the largest possible
                                  % dynamic window, set the angles really big &
they'll be
                                  % shrunk to fit by CheckClipAngles(), below.
else
        rotRate = Radians(9)/frameRate;

        probePositions = tan(Radians( ...
                [0 0]))';

        flowGradient = 0.43/frameRate;

%       foeShift = Radians(24);

        eyeInHeadRots = [0 0 0 0 0];
        bodyRotRates = [-rotRate rotRate 0 0 0];
        simRotRates = [0 0 -rotRate rotRate 0];
        monitorRotates = 1;
        screenSize = [32.4 28.7];
        viewDist = 30;
        wallScaleFactor = 0.8;
% Clip angles were 18 --- KVS 10/21/96
        softClipAngleX = 40;
        softClipAngleY = 40;
end

end

%       eyeInHeadRots = [0];
%       bodyRotRates = [rotRate];
%       simRotRates = [0];

close all
```

```
% Set to 1 to see a plot of the data after each run.
% Probably should set to 0 for naive subjects
plotData = 0;

% numPoints was 200 --- KVS 10/21/96
numPoints = 200;

stimDuration = 0.5; %sec
leadDuration = 0.4; %sec
dotLife = 0.3;              %sec

%flowGradient = rotRate*foeShift + rotRate/foeShift;
%flowGradient = rotRate/(sin(foeShift)*cos(foeShift));

%       eyeInHeadRots = [ rotRate];
%       bodyRotRates = [0 ];
%       simRotRates = [0];
%       probePositions = tan(Radians( ...
%                           [12 0]))';

% QUEST parameters
randomJitter = 0.5;
%randomJitter = 0;
pValue = 0.5;
clipLevel = 0.03;

stimValuesX = tan(Radians([-50:0.5:50]));
stimValuesY = tan(Radians([-30:0.3:30]));
stimValues = [stimValuesX; stimValuesY];

invSlope = tan(Radians(7));
chanceLevel = 0;

% 'terminator' should be set to 'numTrials' to run
% a fixed number of trials, or to [confLevel confLimit]
% for the program to terminate each run when the estimated
% confidence limit (at the 'confLevel' significance level)
% becomes smaller than 'confLimit'
numTrials = 20;
confLevel = 0.05;
confLimit = tan(Radians(4));
terminator = [confLevel confLimit];

scaleType = 'linear';

priorSigmaX = tan(Radians(5));
priorSigmaY = tan(Radians(15));
```

```
responseKeys = ['1' '2' '4' '5' '6'];
feedBack = 0;

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
% Eye trace analysis
if ((eyeTrace)&(strcmp(rotationType,'eye')==1))
        targetDuration = 0.5;
        maxAngle = rotRate*frameRate*(stimDuration+leadDuration)/2;
        numTargets = 5;

        sampleFreq = 60;
        filterSigma = 0.1;
        saccadeCriterion = 0;  % Don't snip saccades
        padSigmas = 3;
        tMin = leadDuration;
        tMax = leadDuration+stimDuration;
        plotFigure = 2;
        traceParams = [sampleFreq padSigmas filterSigma ...
                                                saccadeCriterion tMin tMax plotFigure];

        degRotRate = Degrees(rotRate)*frameRate;
        eyeSpeeds = [degRotRate 0];   % eye either moves at rotRate or is stationary
        eyeMeanMin = [0.8*degRotRate 0];
        eyeMeanMax = [1.25*degRotRate 1];
        eyeMin = [0.67*degRotRate 0];
        eyeMax = [1.5*degRotRate 2];

        speedBounds = [eyeSpeeds; eyeMeanMin; eyeMeanMax; eyeMin; eyeMax];

end


if (strcmp(motionType,'div')==1)
        flowAngle = Radians(0);
elseif (strcmp(motionType,'curl')==1)
        flowAngle = Radians(90);
else                                                    % Spiral
        flowAngle = Radians(45);
end

shiftAngle = rotationAngle-flowAngle;
invSlopes = [invSlope/1.5 invSlope]*[cos(shiftAngle) -sin(shiftAngle); sin(shiftAngle) cos(shiftAngle)];
invSlopes = abs(invSlopes)

simRots = [cos(rotationAngle); sin(rotationAngle)]*simRotRates;
eyeRots = [cos(rotationAngle); sin(rotationAngle)]*eyeInHeadRots;
bodyRots = [cos(rotationAngle); sin(rotationAngle)]*bodyRotRates;
```

```
rotRates = [eyeRots; bodyRots; simRots];

%%%%% Defines %%%%%%

chairAcceleration = Radians(30)/(frameRate^2);

totalDuration = leadDuration + stimDuration;


softClipAngleY = Radians( softClipAngleY );
softClipAngleX = Radians( softClipAngleX );
softClipAngles = [softClipAngleX softClipAngleY];


redMaxLumFrac   = 1;                    % Choose brightness of right eye from 0 to 1.
greenMaxLumFrac   = 0.714;              % Choose brightness of left eye from 0 to 1.
interTrialIndex = 15;                   % Choose brightness for screen shown between
                                                        % trials from 0 to 15. (15 = max.).
redRight = 1;

finalChairPos = Radians( 45 );

%%%%% Switches. %%%%%

startMethod = 'key';        % How does observer initiate a trial?
                                                % ('mouse' or 'key').

viewMode = 'mono';

blankEnd = 0;     % if not 0, blanks dots at end of sequence.

fastLUT = 1;      % uses default values for luminance calibration (1)
                                % instead of reading data from files (0).

INFINITY = 1e10;


%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

stimFrames = round( frameRate * stimDuration );
leadFrames = round( frameRate * leadDuration );
totalFrames = stimFrames + leadFrames;
lifeFrames = round( frameRate * dotLife );

disp(' ');

depth = ScreenTools('GetDepth');
```

```
ScreenTools('SetDepth', 8, 1);

if (~isempty( observer ) )  % If observer is set to '' (empty string), the file name is set to JUNK.mat.

        baseFileName = [observer '_' baseFileName '_' num2str(Degrees(rotRate)*frameRate)];
        pathName = [cd ':Data'];
        fileName = UniqueFileName( baseFileName, pathName )
        tempFileName = [observer '_' motionType '_' num2str(Degrees(rotRate)*frameRate) '_tmp.mat'];
else
        disp('You have not specified an observer.');
        disp('Data will be written to JUNK.mat');
        disp('(Hit any key to continue)');
        pause;
        pathName = cd;
        fileName = 'JUNK';
        tempFileName = [];
end
textFileName = [fileName(1:(length(fileName)-4)) '.txt']

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
%
%       Set up paramTable
%
%       This is a numTrials X numParams matrix; each row
%       contains the values of all the variable parameters
%       for that trial.
%
%       Currently, the arrangement is:
%
%       flowAngle flowGradient focusX focusY eyeRot bodyRot simRot
%
[paramTable, randomIndex, sizeTable] = ConStimParamTable( ...
                                        numRepetitions, ...
                                        rotRates, probePositions );

numConditions = size( paramTable, 1 )
resps = zeros( numConditions, 2 );

numPixels = ScreenTools ('ScreenSizes');    % Set up a fixation cross at the
numPixels = numPixels(screenNum+1,:);

if (strcmp(viewMode, 'mono')~=1)
        eyeSpacing = GetEyeSpacing( observer );    % Look up the IPD for the selected observer.
else
        eyeSpacing = 0;
end
if (any(bodyRots~=0))
```

```
        rotationOffset = GetRotationOffset( observer );
else
        rotationOffset = 0;
end

disp('REMEMBER!');
disp(' ');
disp('If the focus appears to drift over the course of a motion sequence,');
disp('you shoud try to judge where it is at the END of the sequence!');
disp(' ');
disp('Hit any key now to begin');
disp(' ');
EventTools('WaitKey');

disp('Starting experiment.');

ChairInit;
ChairGo;  % pre-load the ChairGo function.

%  Load the red/green color-lookup table.
ScreenTools ('SetScreen', screenNum, 0 )
if (fastLUT==0)
        clut = AnaglyphLUT( greenMaxLumFrac, greenMaxLumFrac, ...
                'calRedG', 'calGreenFG', redRight );
else
        clut = AnaglyphLUT( redMaxLumFrac, greenMaxLumFrac, ...
                'red', 'green', redRight );
end

% Hide the cursor.
CursorTools ('Hide');

if (eyeTrace)
        eyeCalParams = EyePosCal( maxAngle, numTargets, targetDuration, viewDist, ...
                                                        screenNum, numPixels, screenSize,
sampleFreq, ...
                                                        clut );
end

% Run the experiment.

responses = [];
priorDensities = [];
likelihoods = [];
questCompleted = [];
rawFoci = [];
```

```
focusErrors = [];
%focusShifts = [];
respIndex = 1:4;

if (eyeTrace)
        sampInterval = 1/sampleFreq;
        numSamples = ceil(totalFrames *(sampleFreq/frameRate));
        MIOTools('SetupScan',3,[0; 1],sampInterval,numSamples);
end

for i = 1:numConditions
        conditionIndex = randomIndex(i);
        [rots,probePos] = UnpackParams( paramTable(conditionIndex,:), sizeTable );
        eyeRot = rots([1 2]);
        bodyRot = rots([3 4]);
        simRot = rots([5 6]);

        if any(simRot~=0)
                shiftFocus = 1;
%               theRotAngle = atan2( simRot(2), simRot(1) );
%               theShiftAngle = theRotAngle-flowAngle;
%               focusShift = foeShift*[cos(theShiftAngle) sin(theShiftAngle)];
        elseif any(bodyRot~=0)
                shiftFocus = 1;
%               theRotAngle = atan2( bodyRot(2), bodyRot(1) );
%               theShiftAngle = theRotAngle-flowAngle;
%               focusShift = foeShift*[cos(theShiftAngle) sin(theShiftAngle)];
        else
                shiftFocus = 0;
%               focusShift = [0 0];
        end

%       totalRot = simRot + bodyRot + eyeRot;
%       totalRotAngle = atan2( totalRot(2), totalRot(1) );
%       totalRotAngle = totalRotAngle-flowAngle;
%       totalShift = foeShift*[cos( totalRotAngle ) sin( totalRotAngle )];

%       focusShift
%       focusShift = focusShift*[cos(flowAngle) -sin(flowAngle); sin(flowAngle) cos(flowAngle)];
%       focusShifts(conditionIndex,[1 2]) = focusShift;
        %pause
        priorMeans = probePos;
        priorSigmas = [priorSigmaX priorSigmaY];
```

```
        if (~eyeTrace)
        [responseData,priorDensity,likelihood,quests,questCompleted(conditionIndex)] = QuestRun2D( ...
                                                        'SpiralQuestDisplay', stimValues, ...
                                                        invSlopes, chanceLevel, ...
                                                        clipLevel, pValue, randomJitter, ...
                                                        terminator, priorMeans, priorSigmas, ...
                                                        scaleType, responseKeys,...
                                                        feedBack, ...
                                                        probePos, shiftFocus, ...
                                                        flowGradient, flowAngle, ...
                                                        eyeRot, bodyRot, simRot, ...
                                                        chairAcceleration, leadFrames, stimFrames,
...
                                                        frameRate, viewDist, screenNum,
numPixels, ...
                                                        screenSize, numPoints, wallScaleFactor, ...
                                                        blankEnd, softClipAngles, ...
                                                        rotationOffset, monitorRotates, viewMode,
...
                                                        eyeSpacing, startMethod, interTrialIndex, ...
                                                        lifeFrames, finalChairPos );
        else
                if any(eyeRot~=0)
                        theSpeedBounds = speedBounds(:,1);
                else
                        theSpeedBounds = speedBounds(:,2);
                end
        [responseData,priorDensity,likelihood,quests,questCompleted(conditionIndex)] = QuestRun2D( ...
                                                        'SpiralQuestDisplay', stimValues, ...
                                                        invSlopes, chanceLevel, ...
                                                        clipLevel, pValue, randomJitter, ...
                                                        terminator, priorMeans, priorSigmas, ...
                                                        scaleType, responseKeys,...
                                                        feedBack, ...
                                                        probePos, shiftFocus, ...
                                                        flowGradient, flowAngle, ...
                                                        eyeRot, bodyRot, simRot, ...
                                                        chairAcceleration, leadFrames, stimFrames,
...
                                                        frameRate, viewDist, screenNum,
numPixels, ...
                                                        screenSize, numPoints, wallScaleFactor, ...
                                                        blankEnd, softClipAngles, ...
                                                        rotationOffset, monitorRotates, viewMode,
...
                                                        eyeSpacing, startMethod, interTrialIndex, ...
```

```
                                                    lifeFrames, finalChairPos, eyeCalParams, ...
                                                    traceParams, theSpeedBounds, clut );
end

[focusX,confLimit] = QuestThreshold( quests(:,1), stimValues(1,:), likelihood(1,:) );
[focusY,confLimit] = QuestThreshold( quests(:,2), stimValues(2,:), likelihood(2,:) );

focusPos = [focusX focusY];
rawFoci(conditionIndex, : ) = focusPos;

if (shiftFocus)
        totalRot = bodyRot+simRot;
        focusPos = CalcScreenFocus( focusPos, totalRot, ...
                                                    flowGradient, flowAngle );
end

focusErrors(conditionIndex, : ) = atan(probePos)-atan(focusPos);

% convert focus from image coordinates to Radians
% and from retinal to screen coordinates
%focusX = atan(focusX) - focusShift(1);
%focusY = atan(focusY) - focusShift(2);

% Calculate screen errors (in radians)
%focusErrors(conditionIndex, : ) = [focusX focusY]-atan(probePos);

numTrials = size(responseData,1);
responses(1:numTrials,respIndex) = responseData;
respIndex = respIndex+4;
priorDensities = [priorDensities priorDensity'];
likelihoods = [likelihoods likelihood'];

if (~questCompleted)
        disp('ABORTING EXPERIMENT');
        disp([int2str(i-1) ' of ' int2str(numConditions) ' COMPLETED.']);
        disp(['SAVING PROGRAM STATE TO ' tempFileName]);
        eval(['save ' tempFileName]);
        break;
end

if (plotData)
        ScreenTools('SetDepth',8,1);
        subplot(221)
        semilogy( Degrees(atan(stimValues(1,:))), likelihood(1,:) );
        subplot(223)
        semilogy( Degrees(atan(stimValues(2,:))), likelihood(2,:) );
```

```
		subplot(122)
		plot(Degrees(atan(responseData(:,1))),Degrees(atan(responseData(:,3))))
		hold on
		plot(Degrees(atan(responseData(:,1))),Degrees(atan(responseData(:,3))),'g+')
		plot(Degrees(atan(focusPos(1))),Degrees(atan(focusPos(2))),'go')
		plot(Degrees(atan(probePos(1))),Degrees(atan(probePos(2))),'gx')
		plot(Degrees(atan(focusX)),Degrees(atan(focusY)),'g*')
		hold off
		title([num2str(Degrees(focusPos(1))) ', ' num2str(Degrees(focusPos(2)))]);
		pause
		CursorTools('Hide');
		ScreenTools('SetClut',clut);
	end

end

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
%%%%%%%%%%%%%%%%%%%%%%%%%

%%%%% Clean up after animation. %%%%%

MIOTools('Cleanup');

ChairGo(0.0);

ScreenTools ('ShowPage', 0)			% The Macintosh desktop is on page zero.


	% This line prevents the following lines from crashing!!
ScreenTools ('RestoreScreen')

ScreenTools ('SetDepth', depth(1), depth(2))

CursorTools('Init');


%%%%%%%% Save the results to a Matlab format data file %%%%%%%

%%%% UNIT CONVERSIONS %%%%

probePositions = Degrees(atan(probePositions));
flowGradient = flowGradient*frameRate;
flowAngle = Degrees(flowAngle);
rotRate = Degrees(rotRate)*frameRate;
eyeInHeadRots = Degrees(eyeInHeadRots)*frameRate;
```

```
bodyRotRates = Degrees(bodyRots)*frameRate;
simRotRates = Degrees(simRots)*frameRate;
%foeShift = Degrees(foeShift);
focusShifts = Degrees(focusShifts);

paramTable(:,[7 8]) = atan(paramTable(:,[7 8]));
paramTable(:,1:6) = paramTable(:,1:6)*frameRate;
paramTable = Degrees(paramTable);

eyeRots = paramTable(:,[1 2]);
bodyRots = paramTable(:,[3 4]);
simRots = paramTable(:,[5 6]);
probePos = paramTable(:,[7 8]);

focusErrors = Degrees(focusErrors);

softClipAngleY = Degrees( softClipAngleY );
softClipAngleX = Degrees( softClipAngleX );

%%%% WRITE EVERYTHING TO FILE (yes, everything)!!! %%%%
% If there's something you _don't_ want written to file, 'clear'
% it now!

oldPath = cd;
feval('cd',pathName);
eval(['save ' fileName] );
cd(oldPath);

disp(' ');
disp(['Data written to ' fileName]);
disp(['In ' pathName]);
disp(' ');

if (exist(tempFileName)==2)
        disp(['Deleting temporary file ' tempFileName]);
        eval(['delete ' tempFileName]);
end

%%% Write selected data to a text file %%%

dataString = sprintf('%s %s\n','OBSERVER =', observer );
dataString = [dataString sprintf('%s %s\n','DATE =', date )];
dataString = [dataString sprintf('%s %s\n','MOTION TYPE =', motionType )];
dataString = [dataString sprintf('%s %5.2f\n\n','SPEED GRADIENT =', flowGradient )];
dataString = [dataString sprintf('%s\t\t%s\t\t%s\t\t%s\t\t%s\t\t%s\t\t%s\t\t%s\t\t%s\t\t%s', ...
```

```
                                        'Eye Rot.','Body Rot.','Sim. Rot.','Probe Pos.', ...
                                        'Focus Err.')];
dataString = [dataString sprintf('\n')];
for i = 1:numConditions
        dataString = [dataString
sprintf('%5.4f\t%5.4f\t%5.4f\t%5.4f\t%5.4f\t%5.4f\t%5.4f\t%5.4f\t%5.4f\t%5.4f\n', ...
                eyeRots(i,1),eyeRots(i,2), ...
                bodyRots(i,1),bodyRots(i,2), ...
                simRots(i,1),simRots(i,2), ...
                probePos(i,1),probePos(i,2), ...
                focusErrors(i,1),focusErrors(i,2) )];
end

[fid,message] = fopen( textFileName, 'w' );
if (fid==-1)
        disp(message);
        disp('TEXT FILE NOT CREATED');
else
        fprintf(fid,'%s\n',dataString);
        fclose(fid);
        disp(['Data written to file ' textFileName]);
end

disp(dataString);

if (jimCall)
        !calljim
end
```