Evidence of Speed Gradient Sensitive Neurons in the Monkey Extrastriate Area MSTd

Fatemeh Entekhabi

Department of Neurology and Neurosurgery

McGill University

Montreal

May 1996

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements of the degree of Master of Science.

© Fatemeh Entekhabi 1996

National Library of Canada
Acquisitions and Bibliographic Services Branch
395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliotheque nationale du Canada
Direction des acquisitions et des services bibliographiques
395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

The author has granted an irrevocable non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of his/her thesis by any means and in any form or format, making this thesis available to interested persons.

L'auteur a accordé une licence irrévocable et non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de sa thèse de quelque manière et sous quelque forme que ce soit pour mettre des exemplaires de cette thèse à la disposition des personnes intéressées.

The author retains ownership of the copyright in his/her thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without his/her permission.

L'auteur conserve la propriété du droit d'auteur qui protège sa thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

ISBN 0-612-19809-X

Canada

TABLE OF CONTENTS

ABSTRACT

Optic flow is the changing array of light that is reflected from objects in the environment and is projected on the retinae during motion. *Speed gradients* are a natural component of *optic flow* and they are the result of the relative ordering of objects in depth. It has been proposed that *speed gradient* information may signal the direction and speed of self-motion as well as the three-dimensional structure of the environment. The dorsal region of the medial superior temporal area of the visual cortex, or MSTd, is believed to be the neuronal basis for the analysis of *optic flow* and therefore it could convey information about the direction and speed of self-motion and the three-dimensional structure of the environment. In our study, cells in MSTd were tested with random dot stimuli moving at different speeds (*speed gradients*). We found that cells in MSTd are sensitive to stimuli containing *speed gradients*. This supports a role for MSTd in determining the speed of self motion or the three-dimensional structure of the environment or both.

RÉSUMÉ

L'image des objects de l'environnement qui se projette sur notre rétine est continuellement changeante. Ce phénomène est nommé *flux optique*. Une composante naturelle du *flux optique* sont les *gradients de vitesse* qui sont le résultat de l'arrangement des objets à différentes profondeurs de champs. Il a été suggéré que les *gradients de vitesse* fournissent de l'information sur la direction et la vitesse du mouvement propre de l'observateur et sur la structure tridimensionelle de l'environnement. La partie dorsale de la région temporale supérieure médiale du cortex visuel, ou MSTd, est considérée come la base neurologique de l'analyse du *flux optique* et peut donc transporter de l'information sur la direction et la vitesse du mouvement propre et sur la structure tridimensinelle de l'environnement. Dans notre étude, les neurones du MSTd ont été testé par stimulation par des points distribués au hazard se déplaçant à différentes vitesses (*gradients de vitesse*). Nous avons trouvé que les neurones du MSTd sont sensibles aux stimuli contenant des *gradients de vitesse*. Ces résultats supportent le rôle du MSTd dans la détermination de la vitesse du mouvement propre et de la structure tridimensionelle de l'environnement.

1. INTRODUCTION

AND REVIEW

1.1 Area MST and Motion Analysis in the Visual Cortex

1.1.1 Location and Anatomical Connections of MST

Area MST of the superior temporal sulcus of the monkey belongs to the motion analyzing or "dorsal stream" of the visual cortex. MST is located in the upper bank of the caudal STS and in a small portion of the adjacent floor. This area is myeloarchitecturally heterogeneous and includes a small densely myelinated zone or DMZ. The functional significance of this region is unclear. The borders of MST are defined as the projection field to the highly myelinated area MT that forms its posterior boundary. Anteriorly, the lateral boundaries of MST coincides with the medial boundaries of the fundus of superior temporal area (FST). Physiological experiments suggest that the multisensory area posterior parietal (PP) and the superior temporal polysensory area (STP) constitute other borders of MST in the upper bank of the STS (Desimone et. al, 1986).

Retrograde and anterograde injection studies have served as powerful tools for finding the connections of MST to the other regions of the cerebral cortex. Injections indicate direct connections with MT, FST, and PP. Labelling of areas within STP is also observed. The connections of area MST within the parietal cortex include the inferior parietal gyrus (IPG), lateral intraparietal area (LIP), and ventral intraparietal area (VIP). Connections with the temporal area include areas TEO and TF. MST is also shown to project to the dorsomedial part of the frontal eye field (FEF) located within the prefrontal cortex (Boussaoud et al., 1990).

Within MST a dorsal-medial region, or MSTd, and a lateral-anterior region, or MSTl, have been identified. Anatomically, these two subregions show very little

differences except that MSTd has more widespread connections with both the parietal cortex and the temporal visual areas than does MSTl. The differences between these two subregions are mostly physiological. They show differences in the relative frequency and composition of their type of cells with MSTl neurons showing little or no response to rotation or expansion/contraction stimuli. Evidence of retinotopic deficits in pursuit eye movements following lesions of MSTl as well as the finding that many cells in this region respond to small moving spots of light and when electrically stimulated produce acceleration of the pursuit movement towards to side of the brain stimulated, suggest a role for MSTl in maintaining pursuit eye movements. MSTd, on the other hand, shows no effect upon electrical stimulation before and during pursuit task and its neurons are characterized by response to large-field moving random dot patterns with little or no response to small spots of light (Saito et al., 1986; Komatsu et. al, 1989; Tanaka et al., 1989; Boussaoud et al., 1990; Wurtz et al., 1990). More detailed response characteristics of MSTd neurons and their functional role will be discussed later in this chapter.

1.1.2 Parallel Streams in the Visual Cortex and the Processing of Motion

Visual cortex in the macaque comprises 60% of the total surface of the neocortex and it has been divided into 32 areas (Felleman et al., 1991). In the visual cortex, an overall cortical hierarchy is observed whereby the output information of an area is the input of the next higher level area. At each successive level the transformation of visual information occurs and the analysis becomes more advanced. Although hierarchical processing is observed, the visual cortex does not appear to function in a strictly serial fashion. Two major parallel stream of information processing exist in the cortex: the "motion pathway",

or the *dorsal stream*, that projects to the parietal cortex and the "colour and form" pathway, or the *ventral stream*, that projects to the temporal cortex (Van Essen et al., 1983; Felleman et al., 1991). Evidence suggest that the dichotomy in visual information processing begins as early as the retinal levels, continue within the lateral geniculate nucleus (LGN) and further differentiates within V1 and extrastriate visual cortex. At the cortical level the "ventral stream" begins with cells in the interblobs of V1 and the cytochrome oxidase rich blob regions of V1 that project to the interstripes of V2 and the cytochrome oxidase rich thin stripes of V2. The two then heavily project to V4 and further continue to subdivisions of the infero-temporal cortex. The *dorsal stream* of the cortex includes cells in layer 4B of striate cortex that project to the cytochrome oxidase rich thick stripes of V2, followed by V3 then MT, MST and higher processing areas in the posterior parietal cortex (De Yoe et al., 1988). It is suggested that these two streams are associated with different capabilities and types of information they process. The *dorsal stream* is involved in the perception of motion and spatial relationships while the *ventral stream* is associated with the recognition of objects. Support for this hypothesis springs from physiological data that demonstrate the sensitivity of cells in the *ventral stream* to attributes essential for the recognition of objects and analysis of form and colour. For instance, a large proportion of cells in this stream show sensitivity to fine disparity, orientation, and colour, as well as preference for gratings of higher spatial frequencies. On the other hand, in the *dorsal stream*, a large proportion of orientation, direction and disparity selective cells that prefer gratings with lower spatial frequencies is observed. The characteristics of these cells make them ideal candidates for the analysis of motion and spatial relation of objects in space (De Yoe et al., 1988).

Injections of retrograde tracers show evidence of considerable overlap or "cross-talk" between the two parallel processing streams which is suggestive of the integration of spatial and object information at these levels. For instance, dual input from the two pathways in area V4 (however with spatial specificity within V4) is observed. The output from V3 diverges both to areas V4 and MT and from V4 to both parietal and infero-temporal cortex. Similarly, there exists evidence of convergence and lateral connections of inputs between regions and subregions of the two pathways (Baizer et al., 1991).

Clearly, a very large fraction of the visual system is dedicated to motion processing. This is perhaps due to the fact that motion is a fundamental attribute and not simply a displacement of visual image over time. Motion aftereffects are a strong demonstration of this phenomenon: in the "waterfall" illusion for instance, motion and position can only be separate senses since in this situation they are acting in a paradoxical fashion (Nakayama, 1985). Observations of selective impairment of motion perception in humans also indicate that motion is a fundamental biological sense. For instance, in the case of the well studied patient L.M., the tests and CT scans indicate that the area of bilateral lesion in this patient is in the lateral temporo-occipital cortex, an area that is thought to be analogous to area MT of the nonhuman primate. All aspects of the patient's vision is tested normal using the standard visual tests. However, any test requiring the perception of motion fails to produce normal results. The patient perceives movement of objects as a discreet change in position in time with little or no notion of movement. She also shows loss of visual motion after-effects and impairment in perceiving apparent motion (Zihl et al., 1983). Ibotenic acid lesions of motion sensitive areas in the STS of the monkey confirm these findings. After

lesions, the animal is capable of seeing the stimulus (little or no change on the contrast threshold) but not its movement (increase in motion perception threshold) (Newsome et al., 1988; Pasternak et al., 1994).

In the visual cortex, the hierarchical organization of the motion pathway is suggested by the finding that neurons along the serial sequence from V1 to MT and MST analyze motion information over an increasingly large proportion of the retina (increasing receptive field size), respond selectively to more complex motion stimuli, become more directly involved with oculomotor control, and the transformation of information between areas appear to develop new and more complex properties. For instance, in the case of the two consecutive stages MT and MST, evidence suggests that MT is a more general motion-sensitive region of the cortex and it serves to refine and concentrate motion processing for any motion dependent function. In contrast, MST represents a higher level of motion processing and is divided into functionally separate subregions MSTl and MSTd which are used for specific applications of motion information.

Under many experimental conditions, the ability of the visual system to process motion information has been isolated and its properties extensively studied. Many experiments of electrophysiological recordings are performed on behaving (or anaesthetized) monkeys that are visually stimulated by large field information such as optic flow fields.

1.2 Optic Flow: Stimulus for MSTd Neurons

Optic array is the three-dimensional set of light rays reflected onto the retina from

objects in our environment. Changes in the optic array resulting from the movement of the eyes, head, body or by looking at moving objects result in what is termed "optic flow" (Gibson, 1950). Optic flow can be thought of as the field of velocity vectors of light rays that is in a constant state of smooth transformation as a result of the relative motion between the observer and the environment. This changing flow field is defined both spatially and temporally and its pattern depends on the direction of motion and the angle of gaze of the subject. Optic flow patterns present in our environment are the result of complex combinations of rotation of the head or eyes and translation of the subject. The most simple forms are those due to pure rotation or pure translation. For instance a subject moving towards the direction of gaze experiences a flow field that consists of a radial component only. Any changes in a region of the optic flow field can be defined as a combination of four mathematical transformations: *div* or expansion, *curl* or rotation, *trans* or translation, and *def* or shear (change in shape without change in area). *Trans* and *def* have direction and magnitude and are expressed in vector form while *div* and *curl* have only (signed) magnitude and are expressed as scalars. These changes can be thought of as global transformations of local points or events (Koenderink, 1986; Harris, 1994).

Optic flow has been suggested to contain information available to our visual system regarding the three-dimensional structure of objects and the environment as well as on aspects of self-motion (Gibson, 1950). Although classically binocular disparity has been the focus of most studies, it is now a well known fact that motion parallax and optic flow are also significant contributors to our perception of depth. This phenomenon is well demonstrated by the fact that one eyed individuals and animals lacking stereopsis are

perfectly able to navigate effectively in the three-dimensional environment. Motion parallax refers to the relative movement of two object or environmental points caused by the movement of the observer or the objects. It was first noted by Helmholtz:

> "... a person standing still in a thick woods, where it is impossible for him to distinguish, except vaguely and roughly, in the mass of foliage and branches all around him what belongs to one tree and what to another, or how far apart the separate trees are, etc. But the moment he begins to move forward, everything disentangles itself, and immediately he gets an apperception of the material contents of the woods and their relations to each other in space, just as if he were looking at a good stereoscopic view of it." He then further points: "Objects that are nearer appear to move faster, those that are farther appear to move more slowly." (Southall ed., 1925).

Velocity gradients are a component of optic flow and they are a result of the relative distance of objects or surfaces to the observer. When looking at a surface while moving, the parts closer to us will appear to move faster than our point of fixation (which is virtually stationary). Several studies stand evidence for the effectiveness of motion parallax as a source of information that can produce an unambiguous impression of the depth order and shape of objects (Rogers et al., 1979; Braunstein et al., 1988). Many of these experiments are unique in that they use a stimulus that is solely defined by motion parallax, therefore the depth perception is independent of other depth cues such as texture gradients or binocular disparity. The accuracy of judgements, which does not agree in all the experiments, is believed to be based on velocity ratios present in the stimulus display as well as the velocity of the maximum speed in the gradient (Braunstein et al., 1981;

Braunstein et al., 1988; Rogers et al., 1992). The perception of absolute distance of objects from the observer has also been suggested based on motion parallax information alone (Ferris, 1972). However, the data appears to be also dependent on subject-training paradigms and proprioceptive nonvisual factors such as head movements.

In studies aimed at assessing the contribution of optic flow information in the guiding of self motion, computer generated random dot flow patterns are often used that model the velocity vector fields generated on our retinae during motion. Optic flow patterns can generate the illusion of self-motion in a stationary subject and it has been shown that in such situations the thresholds of velocity and luminance for self-motion detection are within the same limits as those for detection of the visual images themselves (Berthoz et al., 1975). Evidence suggests that large field optic flow patterns are, in many viewing conditions, the only necessary source of information for the perception of the direction of heading. For instance, an observer that moves in a rigid environment and who holds the head and the eyes fixed will experience an optic flow pattern that has a radial pattern away from the focus of expansion. In this condition, the focus of expansion indicates the direction of heading for the moving subject. However, in situations where a rotational component is added to the optic flow field, by the movement of the head or eyes while tracking an object on the side, the optic flow pattern is no longer represented in a simple radial form. Several experiments have studied the addition of extraretinal information (such as proprioceptive or "efferent copy" information from the extra-ocular muscles) to the perception of heading. Comparisons between heading judgements while tracking a point and fixating a stationary point with the flow field stimulating the effects

of a tracking eye movements have been performed. Observers accurately judge the direction of self motion based solely on optic flow information provided that the eye movement velocities used are relatively slow (range of 0.2-1.2° per second) (Warren et al., 1988; Warren, Morris et al., 1988). However with higher eye movement velocities, that are more typical of natural conditions (range of 0-5° per second), extra-retinal information about eye position are possibly needed for accurate heading perception (Royden et al.,1992).

In nature, the optic flow patterns experienced by a moving subject are a result of both stationary and moving objects. The vector field resulting from the stationary objects in the environment are purely caused by the motion of the subject whereas moving objects generate motion vectors that are unrelated to ego-motion. In experimental conditions, it has been observed that the accuracy of perception of heading from optic flow remain accurate in the presence of random dot noise or dots with a reduced lifetime. These findings suggest that the points that move independently to the movement of the subject are removed from the analysis of heading from optic flow fields (Van Den Berg, 1992). Additionally, heading accuracies increase as the speed and density of dots in the stimulus is increased with the motion of points at the level of the horizon playing an especially important role in heading perception (Warren and Hannon, 1988; Warren, Morris et al., 1988).

When the direction of self motion is almost perpendicular to the direction of gaze, a more complex pattern of optic flow is generated on the retinae that includes a translational as well as a rotational component. **FIGURE 1** is a simplified illustration of such flow field

that is experienced by a moving observer. What is important to our project is the kind of information that a flow field similar to the one in **FIGURE 1** provides to our visual system. A close observation of this figure shows that the geometric relations among velocity of the image of an object on the retina (γ) at a disparity (α), the velocity of self motion (v), and interocular distance (i) can be given by the equation:

$$v/i = \gamma/\alpha$$

It is thus seen that as the absolute value of α decreases, the velocities of the images (γ) decreases as well. It is clear from the formula as well as the figure that the images of objects located in front of the fixation point move in the direction opposite to the direction of self-motion, and the images behind the fixation move in the same direction as the direction of self-motion. In addition, images that are closest to the fixation point (lower disparities) move at slower angular velocities (shorter arrows) while those farthest away from the fixation (higher disparities) move at faster angular velocities (longer arrows). In this situation, a gradient of speeds and disparities is generated that depend on the positions of the objects in the environment in relation to the observer and the fixation point. Information provided by binocular disparity is, in this situation, a key point to the perception of the direction of heading based on flow pattern alone. Suppose the speed and direction of the objects is all the information available to determine the direction of self-motion. In this situation, the velocity pattern observed could mean that self-motion is to the right (as the diagram depicts) or to the left. Hence, with speed and direction information alone ambiguities arise. On the other hand, suppose that the direction information is tagged with depth information so that the foreground (near disparities) move

to the left (as in the figure) and background (far disparities) move to the right. In this situation, the only possibility is that the observer is moving to the right. Therefore, with disparity information, the problem of heading direction is disambiguated and solved.

Physiological data confirm the above observations. In the dorsal region of area MSTd, 90% of neurons show coarse disparity sensitivity (suggestive of analysis of global motion): 95% of which are either sensitive to near stimuli (near cells) or far stimuli (far cells). The most striking finding is that 40% of cells tested in MSTd preferred one direction of motion when presented with one disparity and the opposite direction of motion when presented with the opposite disparity. These cells are named disparity dependent direction selective or DDD neurons and a large proportion of them respond preferentially to horizontal motion (60% of DDD cells show preference for horizontal axis motion). Additionally most of the MSTd cells show a higher discharge rate when stimuli with higher absolute values of disparity move at faster speeds (Roy et al., 1990; Roy et al., 1992). Looking back at **FIGURE 1**, it is clear that DDD cells are excellent candidates for determining the direction of self motion in such a situation. For instance, the population of cells that respond well to foreground stimuli moving to the left and background stimuli moving to the right are the ones that are activated the most when self-motion is to the right.

In addition to the DDD cells, other evidence has accumulated to support the role of MSTd cells as the ideal candidates for the analysis of optic flow. For instance, MSTd cells prefer large field random dot stimuli and show little response to small spots or bars of light. Their receptive fields are significantly large and sometimes cover half or all of the visual field. They are sensitive to a wide range of stimulus speeds (from 10° to 80° per second)

and are independent of dot density (responding to 350 dots/100°^{2} to as little as 25 dots/100°^{2}). The shape, exact size, and sign of contrast of stimuli are also insignificant factors in determining the magnitude of their response (Saito et al., 1986; Tanaka et al., 1989; Wurtz et al., 1993).

Physiological studies that have revealed the sensitivity of MSTd neurons to changing large field stimuli have confirmed earlier theories that optic flow patterns can be analyzed by relatively simple neural mechanisms (Nakayama et al., 1974). Psychophysical results in humans also indicate the existence of neural mechanisms that integrate motion signals of more complex nature such as rotational and radial motion. For instance, it has been observed that sensitivity of direction of detection, in radial and circular optic flow patterns, increases with increased signal to noise ratio. This finding was measured using stimuli divided into sectors and varying the signal to noise ratio ("noise" included sectors left blank or filled with incoherently moving dots). It is thus suggested that discrimination of direction of stimulus motion takes advantage of signals from all sectors and that specialized detectors (or neurons) that integrate motion signals of different directions from different locations of the visual field exist in the visual system (Morrone et al. 1995). Many neurons in the MSTd region show sensitivity to such components as rotation and radial motion of optic flow fields. Response to contraction or expansion stimuli as well as clockwise and counterclockwise stimuli have been observed in MSTd cells (Saito et al., 1986; Tanaka et al., 1989; Duffy et al. L, 1991). More complex response patterns have also been recorded in MSTd. For instance, double-component (cells that respond to two components of optic flow patterns), triple-components (cells that respond to three

components of optic flow patterns), as well as cells that respond to intermediate stimuli (eg. spiral motion) have been observed (Duffy et al. I., 1991; Graziano et al., 1994). MSTd cells indicate a complex method of analysis and the information coding in this region is perhaps not the function of a single cell but that of a population.

The link between the psychophysical performance and neuronal behaviour is demonstrated in a study where the average psychophysical and neuronal thresholds of MSTd cells to motion perception are measured. It is shown that the behaviour of MSTd neurons in respect to neuronal threshold directly correlated with the psychophysical performance of the animal subject. In some cases, the probability of the animal choosing the preferred direction of the neuron under study increased when that neuron responded more strongly to the stimulus (Celebrini et al., 1994). Similar comparison studies that show a strong correlation between the psychophysical sensitivity of the animal and the sensitivity of individual neurons have been conducted on other motion sensitive areas of the cortex. For instance in area MT it is found that, in most cases, the performance of an individual MT neuron also closely approximates the performance of the monkeys behaviour (Britten et al., 1992). Additionally, microstimulation of MT neurons causes the animal to perceive motion in the preferred direction of the cells stimulated (Salzman et al., 1990; Newsome et al., 1993). These studies are evidence for a link between a specific aspect of perceptual performance and behavioral decision makings to activity within a specific neuronal circuit within the cerebral cortex.

1.3 Goal of Our Project

Speed gradients are a major component of ecological optic flow patterns and their magnitudes and speed ratios are dependent on the three-dimensional organization of the environment and the speed of self-motion. In a speed gradient the images farthest from the fixation point move at faster speeds and those closest to the fixation move at slower speeds. It is thus of much interest to find neurons that respond best to stimuli containing speed gradients. MSTd has proven to be the prime candidate in the analysis of large field stimuli similar to optic flow fields and is therefore the focus of our probing. By finding MSTd neurons sensitive to speed gradients, we can show their potential role in providing information on the three-dimensional structure of the environment and the speed of self-motion.

In a situation where the direction of gaze and the direction of self-motion are perpendicular to each other, the speed gradient magnitude will proportionally increase or decrease (the speed ratios remaining constant) with the speed of self-motion. **FIGURE 2** represents a simplified version of the change in flow field as a result of an increase in the speed of self-motion. Neuronal units that will respond to such change in the flow field will signal and lead to the perception of a change in the speed of self-motion. **FIGURE 3** represents the condition where the speed of self-motion is kept constant but the depth of the objects in the environment is changed. In this situation the speed ratios as well as the magnitude of the speeds are subject to change. Once again, a change in the response of speed gradient sensitive neurons may signal a change in the three-dimensional structure of the environment. Therefore, discovering cells that are selectively responsive to speed

gradients is important in our understanding of the basis of the coding and perception of changes in the environment as well as ego-motion.

It is important to note that with speed gradient information alone the speed gradient sensitive neurons cannot distinguish between the two situations of **FIGURE 2** and **FIGURE 3**. In other words, a cell that responds to a change in the speed of self motion will also respond to a change in the structure of the environment since the two resulting speed gradients (2b and 3b) may be identical in magnitude and their speed ratios. Therefore, with speed gradient information alone, the visual system is unable to decide wether the change is due to a change in speed of self-motion or a change in the three-dimensional structure of the environment. For unambiguous coding by MSTd cells and our visual system, other information or cues need to be introduced. Further approaches to this problem are discussed in Conclusions and Summary.

The data presented in this report supports the hypothesis that MSTd cells are sensitive to speed gradients. It is concluded that they either play a role in signalling the speed of self-motion or the three-dimensional structure of the environment. The possibility that these cells provide both kinds of information cannot be excluded based on our data. The purpose of this project was to look for speed gradient sensitive neurons and by doing so to lay the initial steps that will lead to a multistep study that aims at understanding the analytical methods used by the visual system to code the structure of the environment as well as the speed of ego-motion. The ultimate goal is to find the neuronal basis of these percepts through a series of neurophysiological tests on area MSTd of the Rhesus.

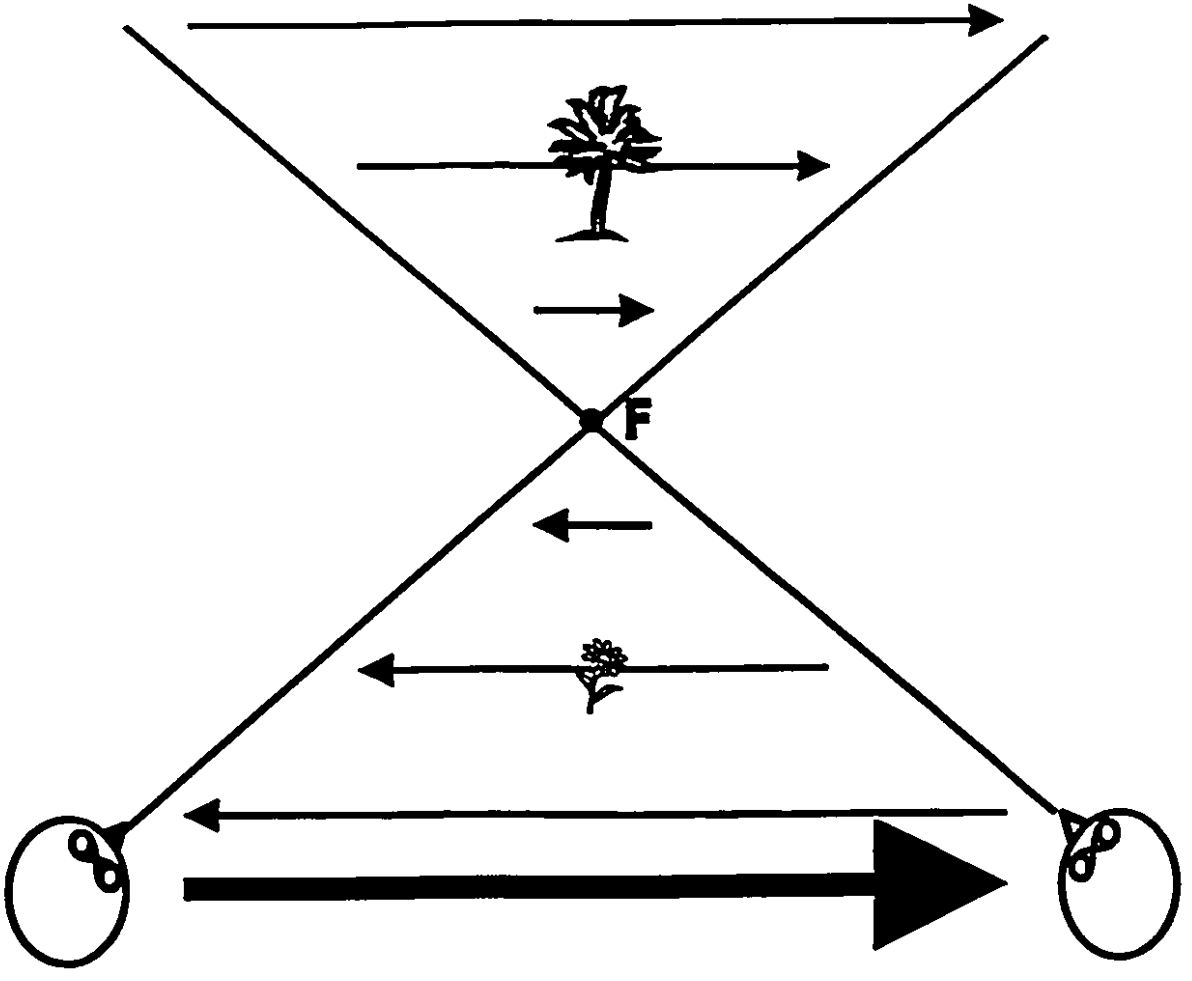

FIGURE 1. A simplified version of the optic flow field experienced by an observer moving to the right (bold arrow) while fixating at a point F. Objects in the foreground move in the opposite direction and objects in the background move in the same direction as the observer. A gradient of speed and disparities is present with objects with higher disparities moving at faster speed (larger velocity vectors).

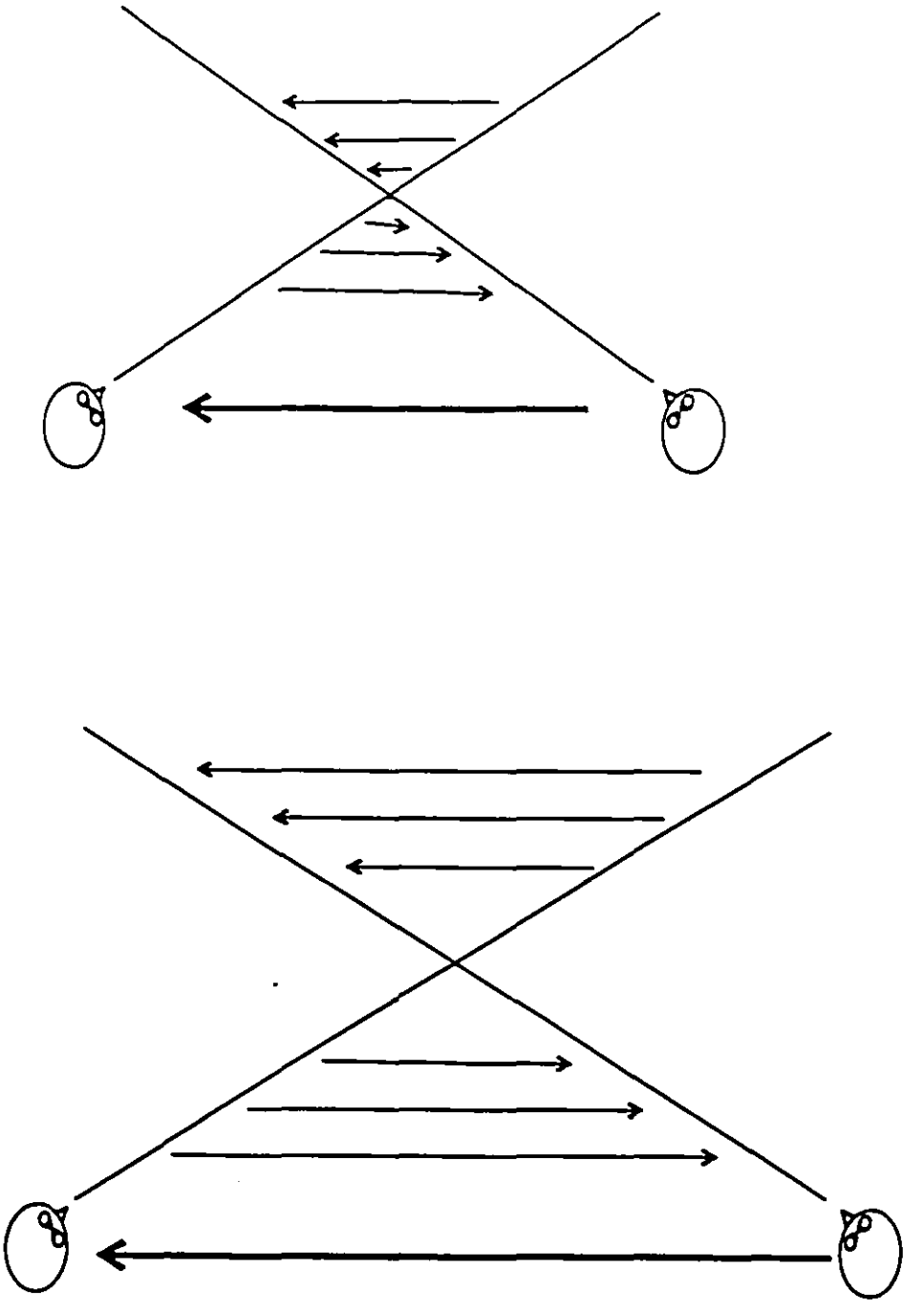

FIGURE 2. 2a) The optic flow pattern resulting from the movement of an observer to the left while fixating on an object at approximately right angle. 2b) The change in optic flow pattern resulting from an increase of the speed of self motion.

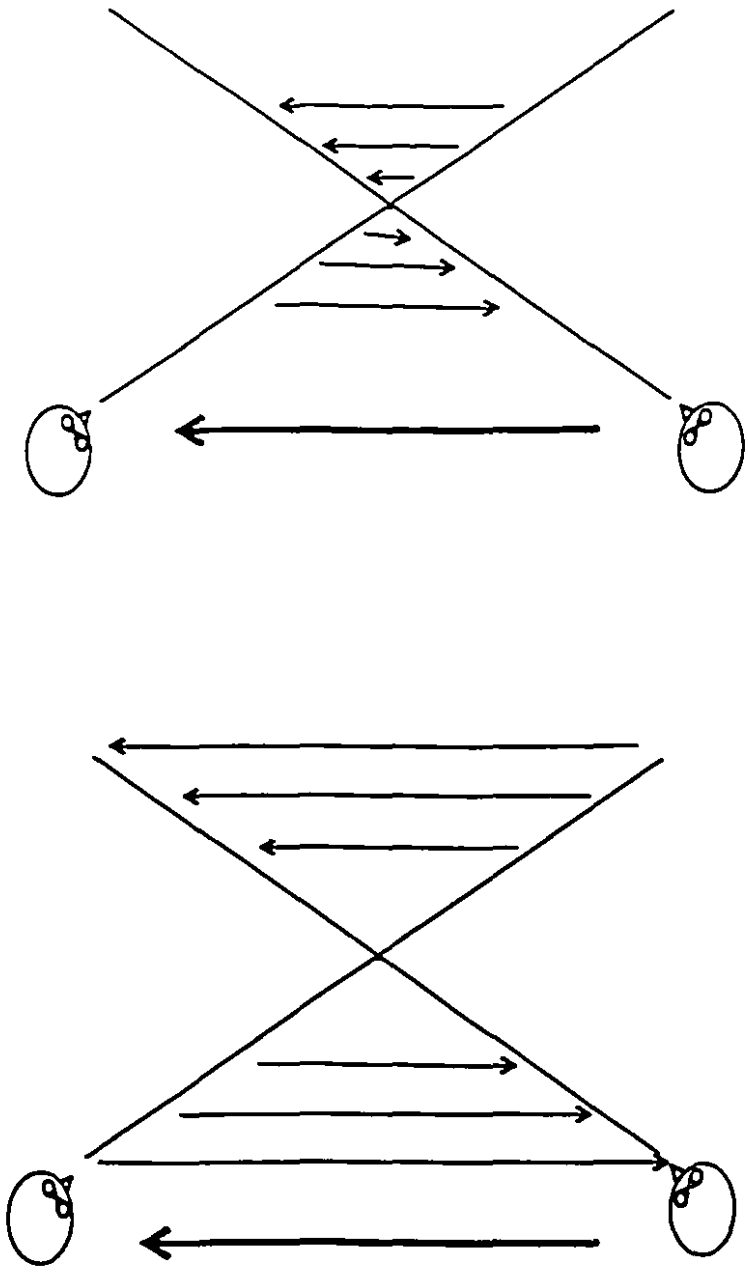

FIGURE 3. 3a) The optic flow pattern resulting from the movement of an observer to the left while fixating on an object at approximately right angle. 3b) The change in optic flow pattern resulting from a change in the three-dimensional structure of the environment.

2. METHODS AND MATERIALS

2.1 Surgical Procedures and Animal Care

2.2 Behavioral Training

2.3 Electrode Penetration and Neuron Isolation

2.4 Visual Stimuli

2.5 Identification of MST

2.6 Hardware and Data Analysis

2.7 Histology

2.1 Surgical Procedures and Animal Care

The animal that served as subject to this study was prepared for electrophysiological recordings by surgically implanting a plastic cylinder and head-holder (Crist Instruments) on its skull. The implant was fortified with the help of surgical stainless steel and titanium screws (8 millimetres in length and 2 millimetres in width) and dental cement. Monitoring of the eye movements was made possible by surgical placing of eye coils under the conjunctiva of each eye. Isoflurane gas was used for general anesthesia during the surgery and all surgical procedures were conducted under aseptic conditions. Post-surgical care included injection of Buprenorphine as an analgesic and oral antibiotic to avoid infection. Following surgery, the cylinders and wound edge were cleaned with saline, hydrogen peroxide, chlorohexidine, and other antiseptic products on a daily basis. All procedures were approved by the Animal Care Committee at McGill and were in accordance with the Canadian Council on Animal Care.

2.2 Behavioral Training

Ten days following the surgery the animal went through several weeks of training and learned to fixate a spot of light while visual stimuli were presented. The method of training was by trial and error learning whereby the animal was rewarded (with fruit, juice, or special animal treats) for every task properly accomplished. During the training and later during recording sessions, the rewards were replaced with juice. The water intake of the animal was controlled and the animal had to earn most of its liquid intakes by performing the fixation task. The water intake during a recording session varied from day to day and

was supplemented at the end of each day to maintain a constant weight. During long holidays or following an operation the animal was provided with water ad libitum. The water control was needed for motivation purposes and performance of the fixation task.

During the recording and cleaning sessions (average six hours per day) the animal sat in a specially designed primate chair and its head was fixed through a head-holder. This procedure allowed little head movements. The monkey was trained to fixate on a dot of light in the centre of a 80°x66° (equivalent to 130x140 cm) tangent screen situated 57 cm away. A reward was granted for each trial during which the monkey's eyes were kept within an approximately 5°x5° area of electronic window surrounding the fixation. If either eye left the window during this period the trial was aborted. The eye movements were monitored using a magnetic search coil apparatus that surrounded the primate chair but did not obstruct the view to the tangent screen.

A set of computer generated stimuli were projected on the screen where the monkey fixated. Each stimulus consisted of a set of overlapping planes of random dots with different values of direction, speed, and disparity. The disparity stimuli were produced by replacing each dot with a horizontally separated pair of dots (green and red) and placing a red filter over the right eye and a green over the left eye of the animal. The following formula was used to calculate the separation between the dots for the desired disparity values

$$\alpha = [\tan^{-1}(i/2f) - \tan^{-1}(i/2d)]$$

where α is the angle of disparity, i is the interocular distance, f is the distance from the midpoint between the animal's eyes to the fixation point, and d is the distance from the

midpoint to the plane of the visual stimulus. For example, for the fixation distance of 86 and an interocular distance of 3.0 cm, a stimuli with 1° crossed disparity would appear to be 30 cm in front of the fixation point.

2.3 Electrode Penetration and Neuron Isolation

A hydraulic microdrive (Narishige) was placed on the recording cylinder and allowed a gentle descent of the tungsten microelectrodes (Frederick Haer) through a stainless steel guide tube. The guide tube was positioned a few millimetres above the location of MST and penetrated the dura. Following the penetration of the microelectrode, a cell's activity was isolated using window discrimination, and magnified and displayed on an oscilloscope. The neuron activity was assessed using an audio monitor and an on-line raster display. The sensitivity of the cell to motion was initially tested by using random dot from hand-held projectors or slits and spots of light from an ophthalmoscope. Cells that were not motion sensitive were not further tested. The receptive fields locations and extent were determined by moving the stimuli away from the centre of the field until the cell no longer responded. The receptive field was marked on the screen and its eccentricity determined. Its size was estimated as the square root of the area and the eccentricity as the distance between the centre of the field and the fixation point. The computer generated stimuli were then projected on the screen and the cell's properties were further tested.

2.4 Visual Stimuli

Each stimulus was randomly displayed for an average of one second. The response

to each stimulus was viewed as a raster or a histogram. Dot number for all stimuli was 300 dots per stimulus so that the density of the dots varied with the size of the receptive field. In stimuli with speed and disparity gradients, the random dot planes closest and farthest away from the point of fixation (higher disparities) moved at a faster rate than those closest to the point of fixation. Three types of stimuli were used in these experiments that tested disparity tuning, speed gradient sensitivity, and speed tuning of the cells.

DISPARITY TUNING TESTS. The disparity tuning was examined using six stimuli of single planes moving in the preferred direction of the cell at six disparities: crossed 1°, 2°, 3°, and uncrossed 1°, 2°, 2.5°.

SPEED GRADIENT TESTS. The tuning to speed gradient was examined by using the 5 different pairs of stimuli that moved in the preferred direction of the cell. Each pair consists of a control stimulus (containing no speed gradient) and a stimulus with planes moving at different speeds:

pair 1: stimuli (3 planes) containing disparity gradients with and without speed gradient
pair 2: stimuli (3 planes) moving at one disparity with and without speed gradient
pair 3: stimuli (3 planes) moving at the plane of fixation with and without speed gradient
pair 4: two plane moving in opposite directions with and without speed gradient
pair 5: a single plane moving in one direction with or without speed gradient

SPEED TUNING TESTS. The speed tuning was examined by presenting 10 stimuli moving at different speeds (including 0°/sec) at 0° disparity. The speeds tested include: 10°, 20°, 30°, 40°, 50°, 60°, 80°, 100°, 120°, and 0°/sec.

2.5 Identification of MST

MST was located using a magnetic resonance image of the animal's brain that

allowed visualization of the superior temporal sulcus (STS). The physiological properties of the neurons were also used to confirm the area of recording.

IDENTIFICATION BY MRI. After surgery, the monkey was anaesthetized and a magnetic resonance image of its brain was obtained. Although MST itself could not be seen in the MRI, its approximate location within the STS was estimated by identifying and assigning coordinates to this sulcus. Upon examination of the images, the STS and middle temporal (MT) area were localized. MT could be localized on the posterior bank of the STS because of its high myelin content. The distance from MST to the centre of the recording cylinder (reflected as a shadow on the image) was also measured.

IDENTIFICATION BY PHYSIOLOGICAL PROPERTIES. In all the experiments, the electrodes penetrated vertically in the direction of MST. Cells were tested for properties such as response to large field stimuli, disparity, and size of receptive field that could distinguished them as MST neurons.

2.6 Hardware and Data Analysis

The paradigm, storage, and immediate display of the data were controlled by a real-time experimental software, REX, which ran on a 486-PC computer. The large field random dots were generated by a PC-286-based microcomputer and projected onto the screen using a TV projector (Electrohome ECP 3100). The data for each cell was collected in separate files and analyzed using MATLAB. Activity of a cell in response to a stimulus was measured in terms of number of pulses or spikes in the time window during which the stimulus was presented. The first 400 milliseconds was excluded from analysis to remove

the strong "ON" or phasic response that was typically present following stimulus presentation and was less selective for the type of stimulus presented. The response between 400-1000 millisecond was then averaged over n trials (n = total number of trials of the cell's response to one presentation of one stimulus). Graphs and figures were then made using MATLAB and COREL software packages.

2.7 Histology

Since the monkeys is still alive and used for further testing, histological confirmation is not available. However, we believe that the application of the MRI and physiological testing has provided satisfactory results in the identification of MST.

3. RESULTS

3.1 Disparity Sensitivity

3.2 Speed Gradient Sensitivity

3.3 Speed Tuning

Following isolation of a neuron, several tests were conducted in order to determine its physiological properties and confirm its location in MSTd. First the directional selectivity and the response selectivity to random dot stimuli or small slits/spots of light were tested. Then the size and the location of the receptive field were determined using the steps described in Methods and Materials. A cell showing no visual response was not further tested. 13 directional selective cells that preferred large field random dot stimuli were isolated and tested in one hemisphere of the Rhesus monkey. All had receptive fields typical of MSTd that covered a large portion of the contralateral visual field and that came close to or included the fovea.

3.1 Disparity Sensitivity

A neuron is considered disparity sensitive if it shows a significant increase in neuronal response to a stimuli having different horizontal disparities. To determine if a cell is disparity sensitive a disparity index is used that is defined as: $DI = 1-(N-S)/(P-S)$ where P is the average of the discharge rates for the preferred disparities (crossed or uncrossed), N is the average of the discharge rates for the non-preferred disparities, and S is the average of the spontaneous activity (before stimulus onset). A DI of 0.2 or more is taken as an indication of the disparity sensitivity of a neuron. DIs of larger than 1.0 indicate neurons that show an increased discharge rate for the preferred disparities and a decreased discharge rate below spontaneous for the non-preferred disparities. We have found 5/13 neurons that show far or near tuned disparity sensitivity typical of area MSTd. The DIs of the cells in this study are shown in **TABLE 1.** Most cells showed a DI of 0.3 and only 1 had a DI

larger than 1 (DI= 5.7). **FIGURE 4** shows a far neuron (preference to all uncrossed disparities of 1°, 2°, and 3° present in the stimulus) with a DI of 0.3.

TABLE 1. Disparity indexes of the recorded disparity sensitive neurons

Neuron #	al 3	al 5	al 6	al 8	al 12
DI	5.7	0.2	0.3	0.3	0.3

In a previous study on MSTd (Roy et al., 1992), from a sample of 272 neurons over 90% showed sensitivity to binocular disparity and 95% of disparity sensitive neurons were either far or near cell presented at equal frequency. In our sample only 38.5% of cells were disparity sensitive and all preferred crossed stimuli (far cells). These findings raises questions about the location of our recording electrodes in relation to MSTd. Two possible explanations may help to clarify the situation. Firstly, the sample size used in this study is relatively small compared to typical studies. The number of recorded neurons has been limited as a result of the many technical problems that arose during the two years of recording from two different primates. The first primate used was euthanized at the end of the first year and is believed to have had an abnormally small (or none at all) MST area. This unusual situation has also been observed in other laboratories using nonhuman primates (personal communication with Dr. Tanaka). The results from the first animal is not included in the Thesis. The second primate provided us with the results presented here. However, the implantation procedure on this primate (MRI compatible plastic head equipment and the initial use of fewer head screws) was experimental and caused many

inconveniences during the recording period (detachment of the implant and the eyecoils happened a number of times). Based on such a small sample size only weak statistical statements on the population of cells in MSTd can be made. Secondly, the small percentage of disparity sensitive neurons observed may be because despite our careful estimations from the MRI and targeting of MSTd, we might not have been in the predicted area at all times. However, the possibility of this is rather slim since all but only 3 of the cells were recorded from the same guide tube at approximately the same depth. More specifically, 10 cells were recorded at a depth of 8.75-12.75 mm below the edge of the guide tube, only one was recorded at 16.75 mm, and the other 2 cells were at unknown depths. It should be noted that the above measurements and the starting point of an electrode at the edge of the guide tube are only estimates with a 4-5 mm variability from one recording session to the next. Hence the possibility that the neurons were recorded from different cortical areas is highly unlikely and the disagreement between the percentage of disparity cells in our sample with the ones of other studies is likely due to the statistical limitations of a small sample.

3.2 Speed Gradient Sensitivity

To statistically test the significance in the increase of the discharge rate of a neuron in response to a speed gradient test, the *student t test* with a confidence interval of 95% ($p = 0.05$) was used. The stimuli used to test sensitivity to speed gradients have been previously described to be 5 pairs of control and speed gradient containing stimuli (the existence of the 5 different pairs of stimuli has no relevance to the results presented in this Thesis and the appearing redundancy is due to the changes of project aim that took place

along its course). Data on speed gradient testing is available in only 11 neurons with some being tested with three and others with all 5 of the test pairs. A neuron that responded to at least 1 in 5 of the stimuli was considered speed gradient sensitive. The responses of the neurons to speed gradients were found to be both excitatory and inhibitory. A total of 3 cells in this sample showed a significant increase and 4 neurons showed a significant decrease in activity to speed gradients as compared to control stimulus. 1 of these neurons (neuron al8) shows both excitatory and inhibitory responses to speed gradients. **FIGURES 5, 6 and 7** show the neurons that are stimulated by speed gradients. **FIGURES 8, 9, 10 and 11** show the neurons that inhibited by speed gradients. The analytical power and significance of the inhibitory type of neuronal behaviour is unclear. One possible theory might be that this kind of inhibitory signalling may play a role in the population coding of a group of speed gradient sensitive neurons by accentuating the response of a complimentary sets of neurons sensitive to the a closely related speed gradient stimulus.

3.3 Speed Tuning

Data is available on only 2 speed gradient sensitive neurons. **FIGURE 12** shows the results of the testings. The test for speed tuning has already been described in the Methods and Material. Both neurons show a very similar type of broad tuning with a slight shift towards slower speeds. The purpose of testing the speed gradient cells for speed tuning is to eliminate a possible interference of the preferred speed of the neuron in the responses recorded during speed gradient tests. In other words, if a narrow speed tuning or a preference for a particular speed is observed in a cell, it would be necessary to test the

cell for speed gradient sensitivity at preferred as well as non-preferred speeds. In the 2 cells tested for speed tuning it is clear that the increased discharge rates of neurons tested for speed gradient sensitivity are not a result of the presence of the referred speed of the neuron since the neurons have a rather broad speed tuning curves. It is thus confirmed that the responses seen earlier, are purely due to the presence of speed gradient information in the stimuli.

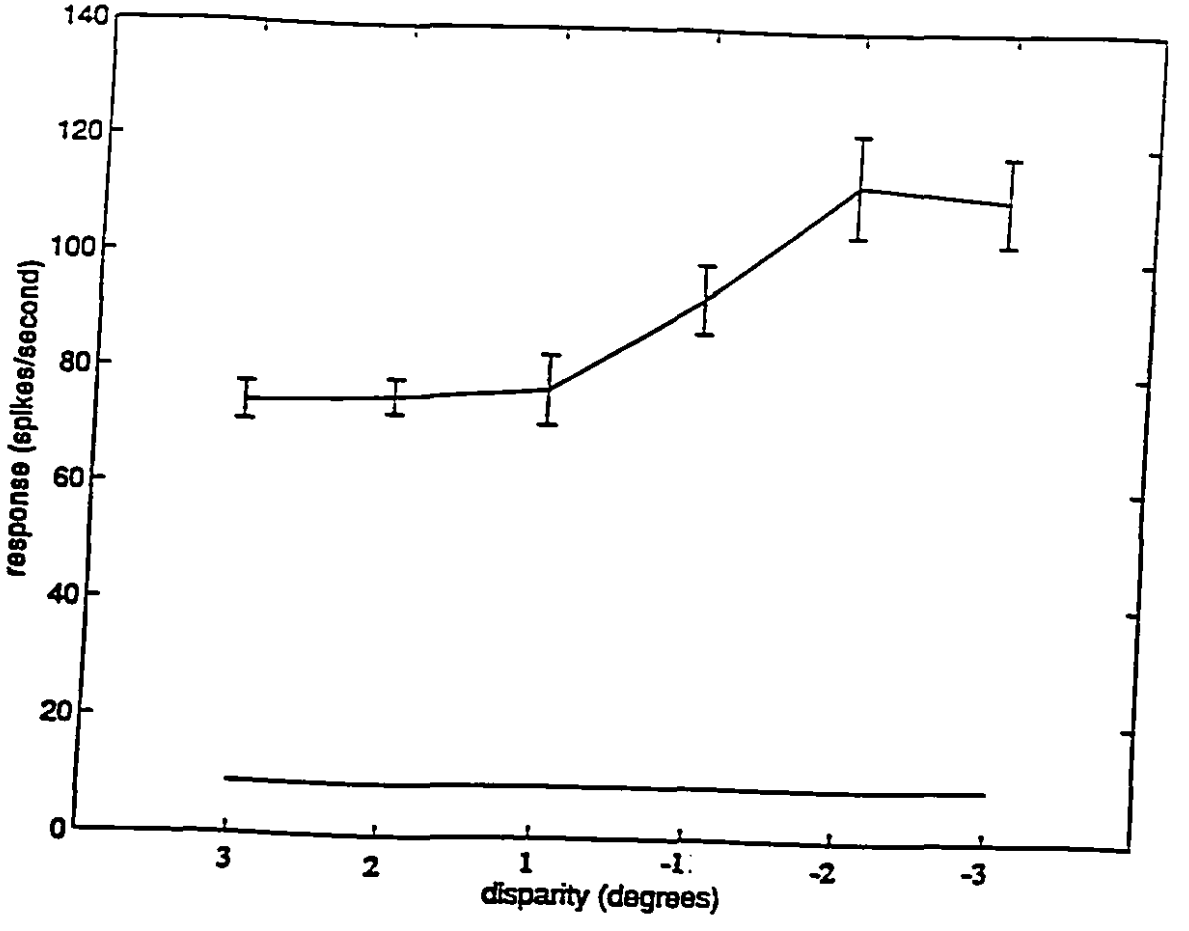

FIGURE 4. A disparity sensitive far neuron with a disparity index of 0.3. On the horizontal axis are the 6 different disparities and on the vertical axis is the discharge rate in spikes per second. The cell shows increased response above spontaneous (straight line) to all uncrossed disparities of a stimulus moving in its preferred direction (270 degrees).

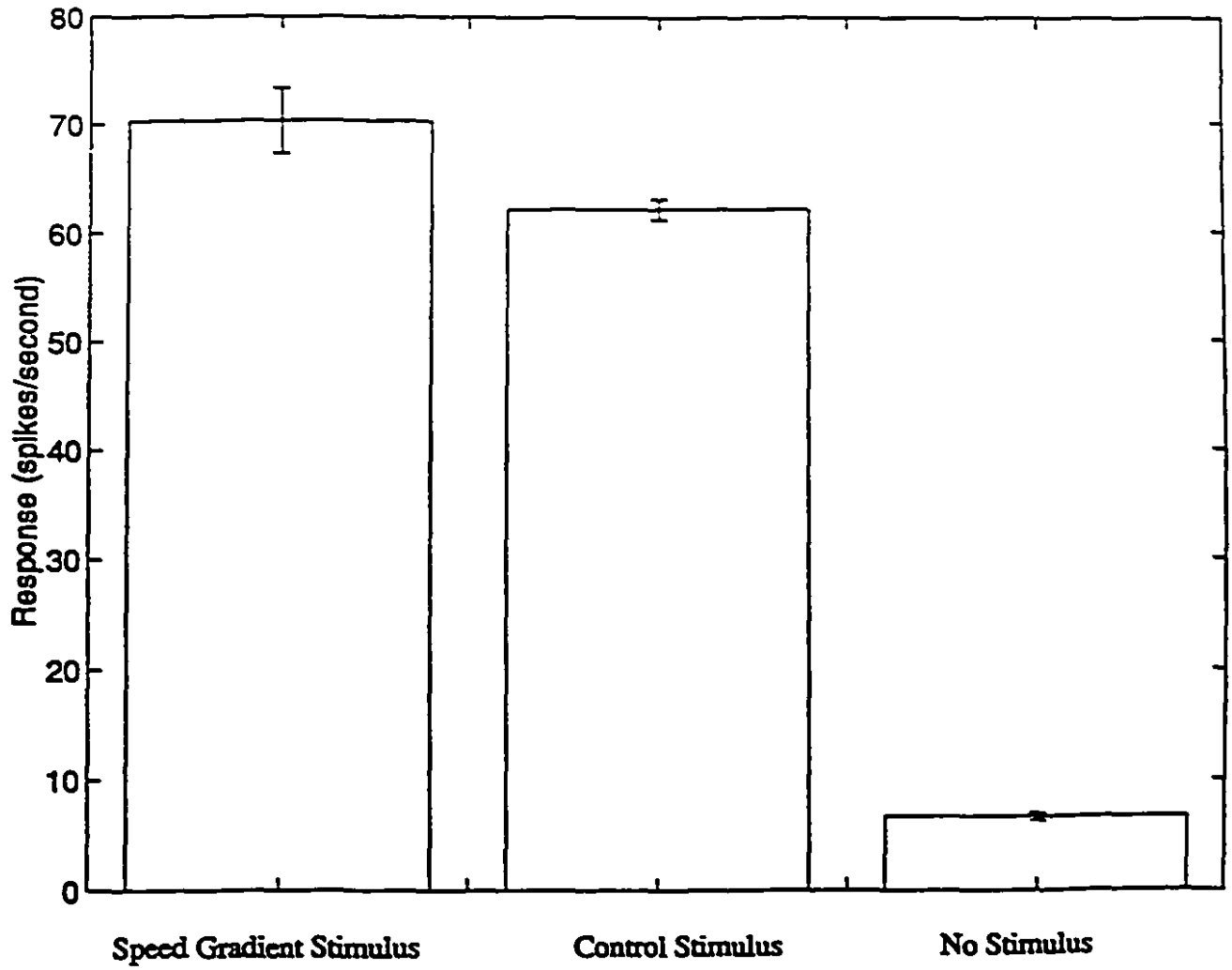

FIGURE 5. Cell all shows a 13.2% increase in discharge rate from control when presented with speed gradients. The stimuli used here was made of three planes moving at the same uncrossed disparity in the preferred direction of the cell.

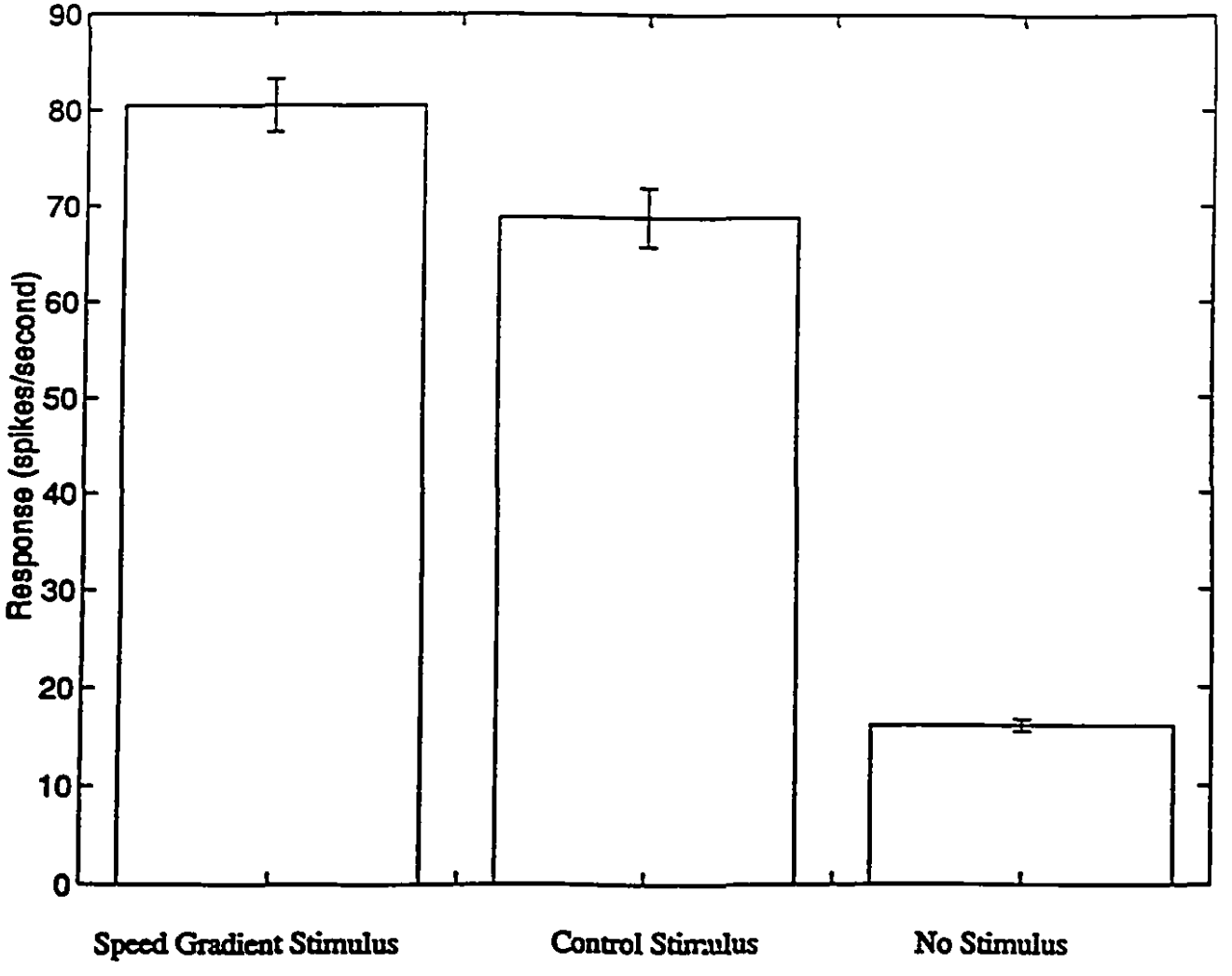

FIGURE 6. Cell al3 shows a 17.0% increase in discharge rate from control when presented with speed gardients. The stimuli used here was made of two planes moving in opposite directions at 0 disparity.

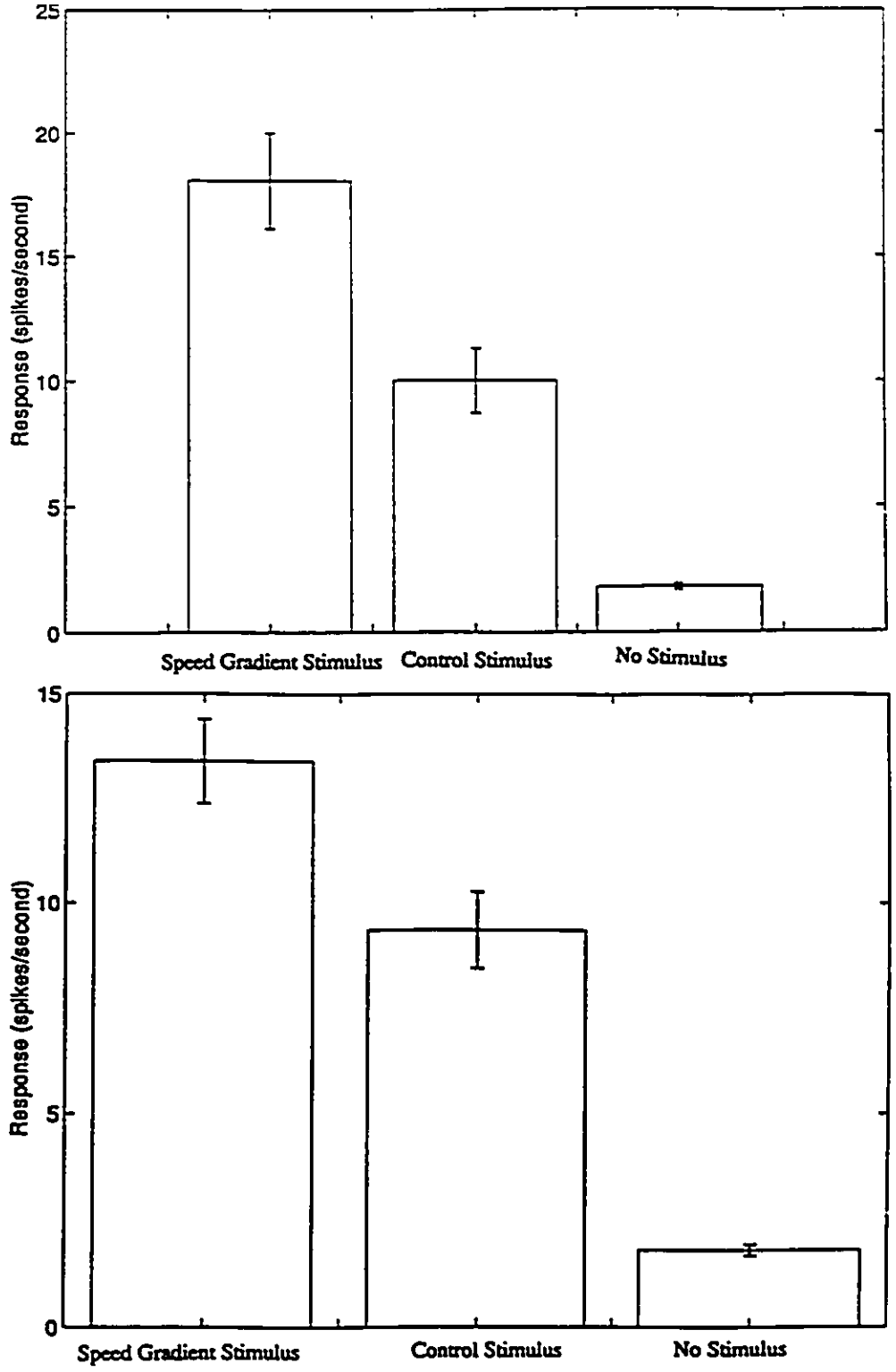

FIGURE 7. Response of neuron al8 to two separate pairs of speed gradient stimuli. This cell shows an 80.1% increase when both the control and test stimuli contained a disparity gradient (top figure). The same neuron shows a 43.0% increase discharge rate when both control and test stimuli were at one single crossed disparity (bottom figure).

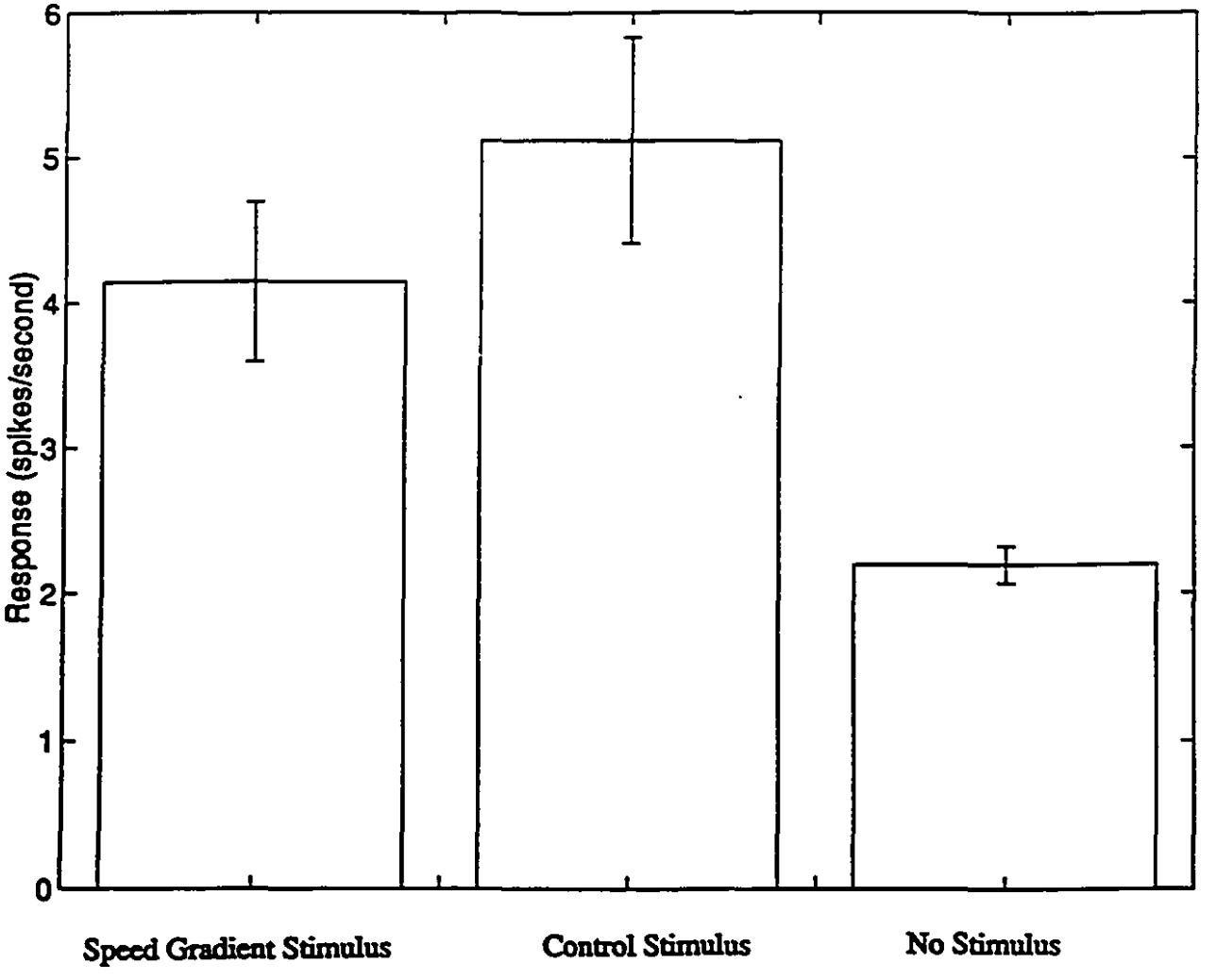

FIGURE 8. Cell al2 shows a 19.1% decrease in discharge rate from control when presented with speed gardients moving in the preferred direction of the cell. Both the control and test stimuli contained disparity gradients.

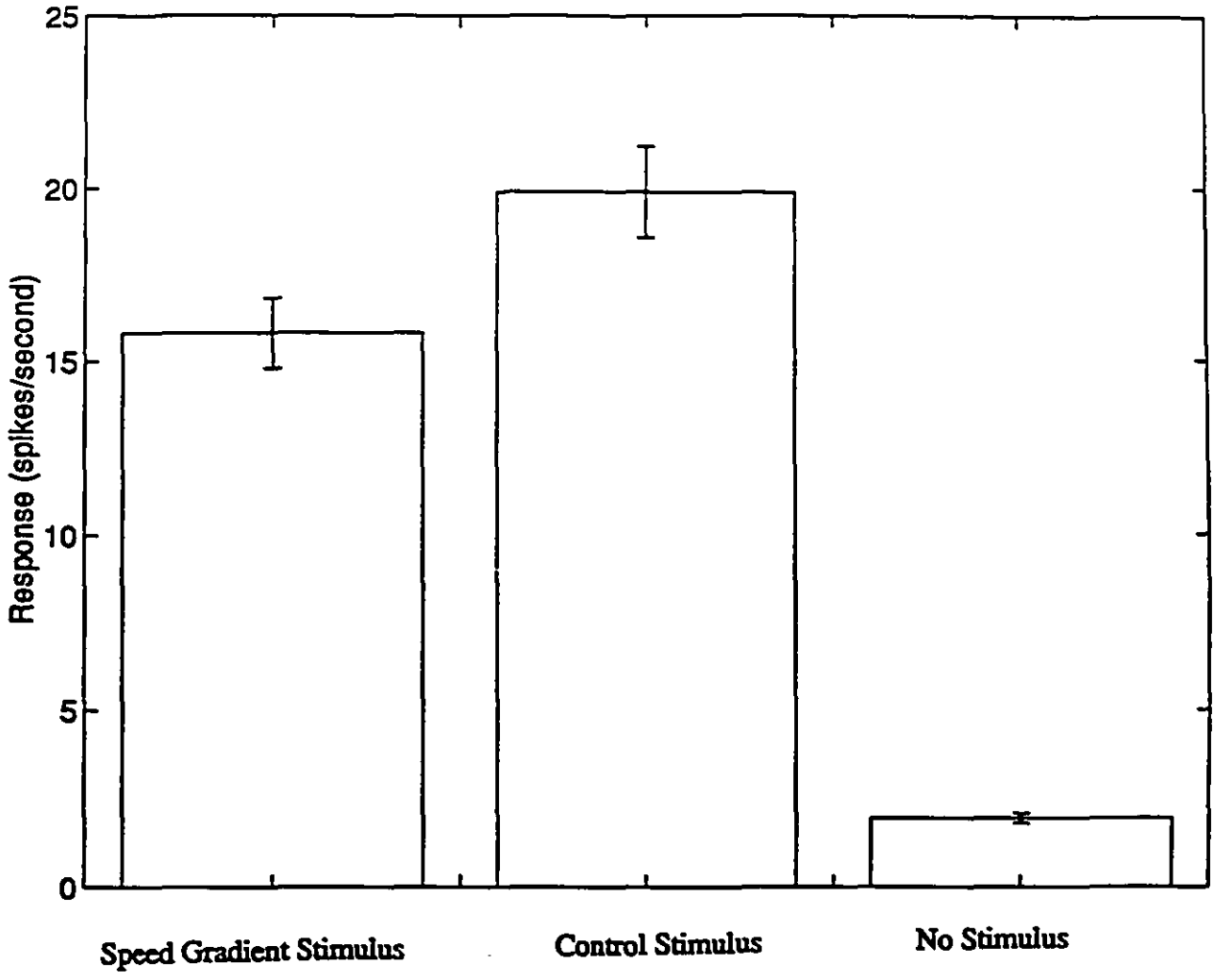

FIGURE 9. Cell al8 shows a 20.5% decrease in discharge rate from control when presented with speed gardients. The stimuli used here was made of planes moving in the prefered direction of the cell at 0 degrees disparity.

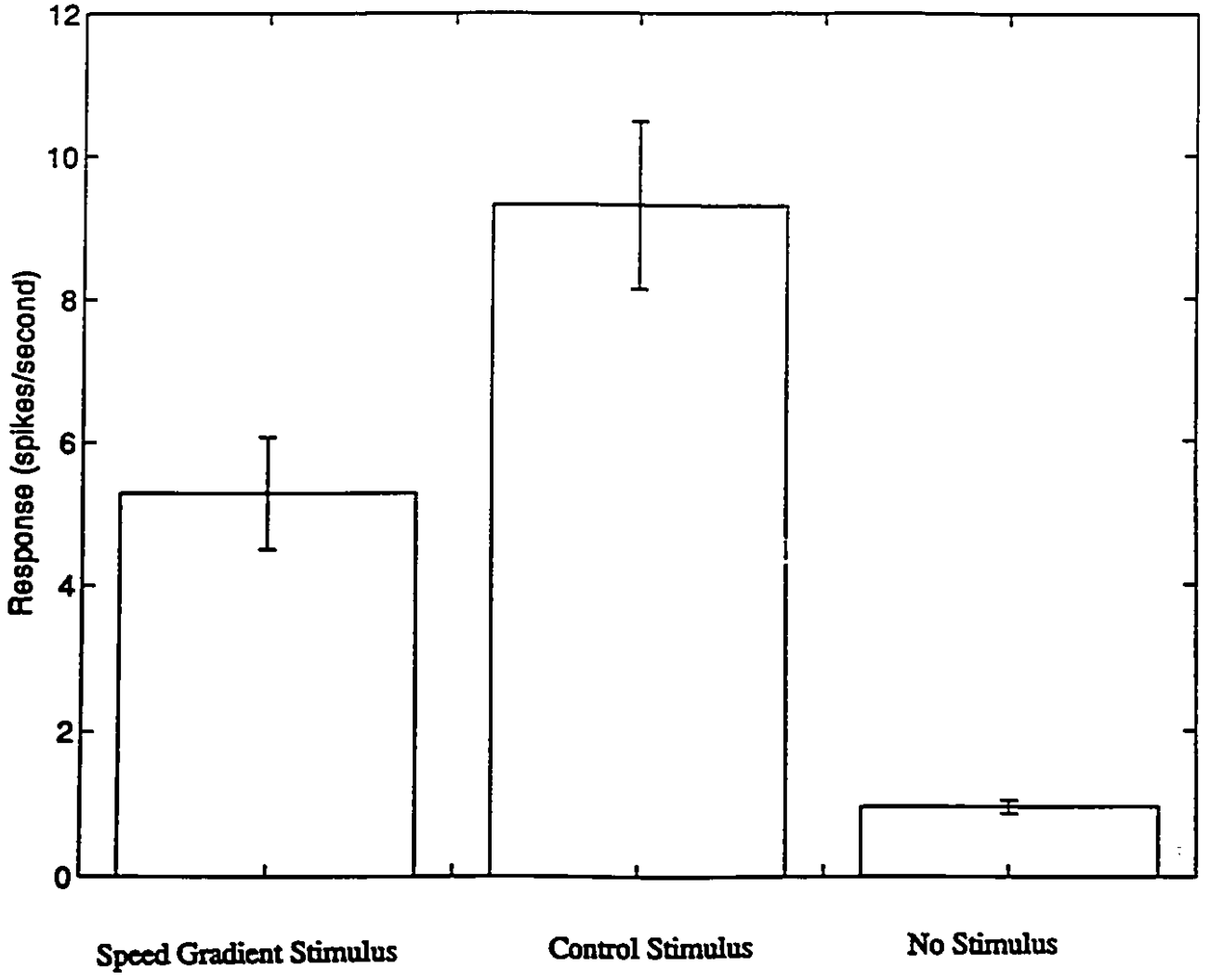

FIGURE 10. Cell al9 shows a 43.2% decrease in discharge rate from control when presented with speed gardients. The stimuli used here was made of two planes moving in opposite directions at 0 disparity.

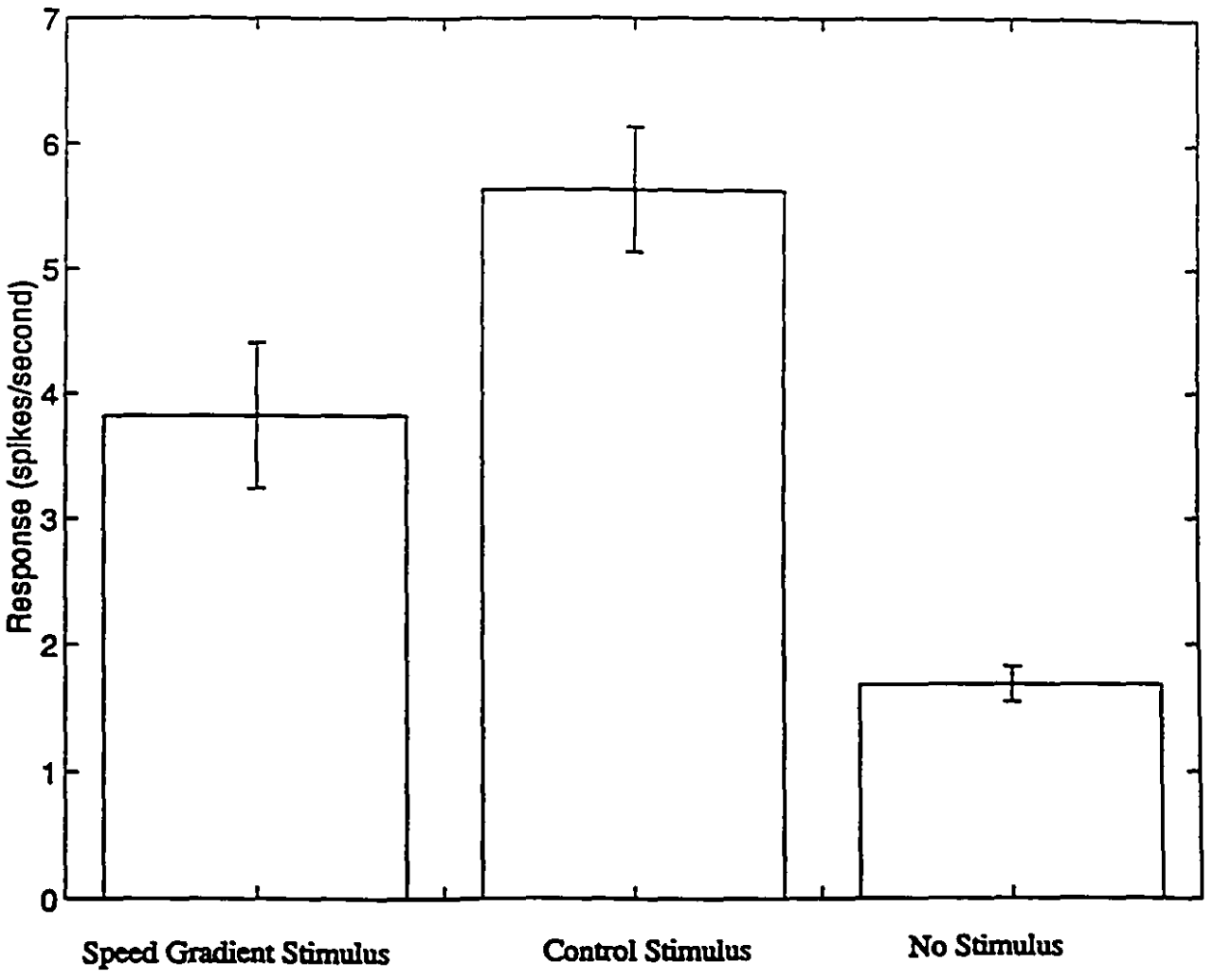

FIGURE 11. .Cell al10 shows a 32.1% decrease in discharge rate from control when presented with speed gardients. The stimuli used here was made of planes moving in the prefered direction of the cell at 0 degrees disparity.

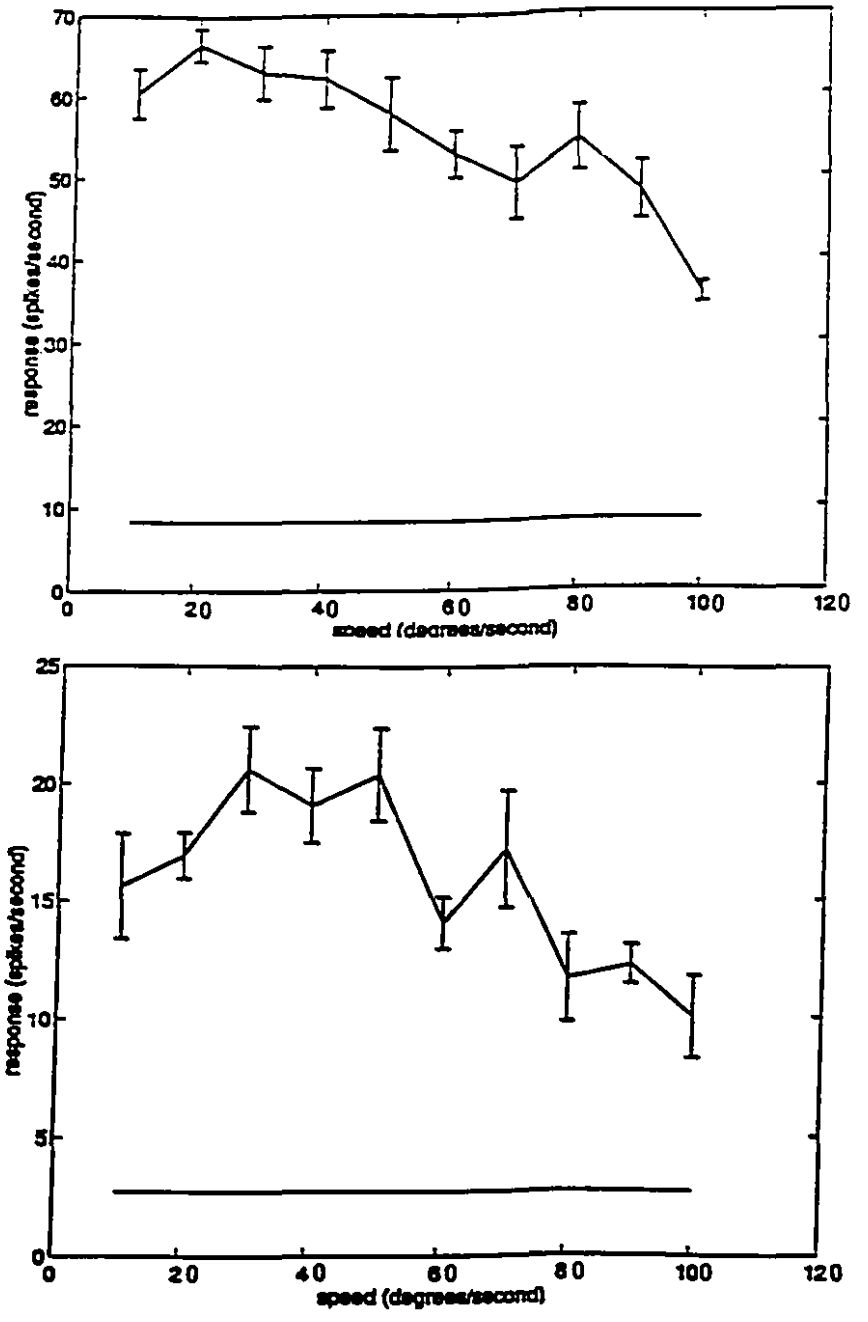

FIGURE 12. The response of two speed gradient sensitive MSTd neurons (cells al1 top figure and cell al3 bottom figure) to speed tuning stimuli. The horizontal axis represents 10 different speeds in degrees per second (including a stationary stimulus) moving in the preferred direction of the neuron. The vertical axis shows the response in spikes per second. Both neurons show a broad speed tuning curve with a slight shift towards slower speeds.

4. CONCLUSIONS

AND SUMMARY

In this study, neurons in area MSTd in the parietal cortex of the rhesus monkey have been tested. 3 neurons showed a significant increase and 4 showed a significant decrease in activity when stimulated with speed gradient information as compared to control. Speed gradients are a common component of natural optic flow and they are the result of the motion between the subject and the objects located in a three-dimensional arrangement. For instance in **FIGURE 1** the motion of the observer causes the images of objects the foreground and background to move at different speeds on the retina creating a speed gradient. Theoretically, speed gradient information can provide the visual system with cues signalling the speed of self motion as well as the three-dimensional arrangement of the environment. The speed gradient sensitive cells found in MSTd confirm this theory and provide the biological basis for this type of analysis by the visual system. For instance, if a moving observer with a gaze direction approximately perpendicular to the direction of self-motion increases their speed, as in **FIGURE 2**, then an increase in firing rate of appropriate neurons may take place. Thus cells sensitive to faster speed gradients will start firing as a result of the increase in the speed of the observer. A similar change in firing rate of cell populations might take place in a situation where a change in the three-dimensional arrangement of the environment takes place. This situation is depicted in **FIGURE 3** and will result in an identical neuronal response as in the first situation. Our findings of neurons that respond to speed gradient information is of great importance however speed gradient sensitivity alone does not distinguish the neuronal response caused by a change in speed of self motion and that of a change in the three dimensional structure of the environment. To disambiguate the situation, the visual system needs other types of information and cues. A

possible informational candidate that may provide, in conjunction with speed gradient information, more specificity to the response of these neurons is binocular disparity. Cells in area MSTd do show a response to binocular disparity hence it is natural to look for a possible interaction of disparity and speed gradient information at a neuronal level.

Refer back to the formula introduced earlier in Introduction and Review: $v/i = \gamma/\alpha$ where v is the velocity of self motion, γ is the velocity of the image of an object on the retina at a disparity α, and i is the interocular distance. Since interocular distance does not change for a subject we can conclude that the speed of self motion is dependent on the ratio between speed and disparity. In other words, the speed of self motion is not coded by a change in the speed of the image of the object per se but rather it is coded by the speed of the image of the object in depth. Therefore, neurons that respond to different values or a narrow range of angular speed to disparity ratios (γ/α) can unambiguously signal the speed of self motion. A possible sets of stimuli for finding MSTd neurons sensitive to γ/α can be a set of planes moving at a range of different speed/disparity ratios. For instance with a speed of self motion of 1 m/sec (v = 1 m/sec) and an interocular distance of 4 cm for the monkey ($i = 4$ cm) one may calculate the following:

for $\alpha = 0°$, $\gamma = 0°$/sec
$\alpha = 1$ or $-1°$, $\gamma = 25°$/sec
$\alpha = 2$ or $-2°$, $\gamma = 50°$/sec
$\alpha = 3$ or $-3°$, $\gamma = 75°$/sec

Similarly, for a speed of self motion of 0.1 m/sec and 10 m/sec (one order of magnitude smaller and larger respectively) the following is calculated:

at 0.1 meters per second:
for $\alpha = 1$ or -1°, $\gamma = 2.5$°/sec
$\alpha = 2$ or -2°, $\gamma = 5.0$°/sec
$\alpha = 3$ or -3°, $\gamma = 7.5$°/sec

at 10 meters per second:
for $\alpha = 1$ or -1°, $\gamma = 250$°/sec
$\alpha = 2$ or -2°, $\gamma = 500$°/sec
$\alpha = 3$ or -3°, $\gamma = 750$°/sec

The three sets of stimuli presented are seen as containing three planes of random dot stimuli moving at different speeds in depth. They provide a model for the optic flow experienced by a moving observer (similar situation as in **FIGURE 1**) at the three different speeds of self motion (1, 0.1 and 10 m/sec respectively). By finding neurons that preferentially respond to a specific range of speed/disparity ratios (or in other words, cells that are tuned for a specific rage of γ/α) we would be able to provide evidence for the hypothesis that the visual system, and neurons in area MSTd, use this method of analysis to signal the speed of self motion.

A second type of MSTd speed gradient sensitive neurons that specifically and unambiguously code for the three-dimensional structure of the environment of a moving observer may exist. Such cells may be tuned for specific speed ratios. This hypothesis is based on the relation between the depth of an object relative to another and their speeds of motion on the retina of a moving subject. For instance two depth planes move on the retina at two different speeds and the ratio of the distance between the two depth planes is directly proportional to the ratio of their speeds. The speed ratios therefore signal the distance of the two depth planes (or objects in depth) relative to one another. This critical parameter of speed ratios can provide valuable information on the relative distances of objects and the structure of the environment. Since speed gradient sensitive cells have been found in area MSTd, the next step in finding cells that unambiguously signal the structure of the

environment is to test the sensitivity of these cells to specific speed ratios and determining their tuning curves for this parameter. The hypothesis is that some neurons in MSTd are differentially tuned to different ranges of speed ratios. The type of stimuli that may be used to test neurons in MSTd could be two or three moving planes with speed ratios of 1:1 to 1:10. For instance in a three plane stimulus (the visual system is most likely to compare the speeds of at most three objects at any single time) a stimulus with speed ratio of 1:5 contains three planes moving at 1°, 5°, and 25° per second. This stimulus will in turn signal three planes or objects where the closest is at 1/5 a distance as the second which in turn is at 1/5 a distance as the farthest. Finding cells that are tuned for speed ratios will provide strong evidence in support of the ability of neurons in area MSTd in processing the relative distances of objects and therefore signalling the three-dimensional structure of the environment.

In conclusion, by finding cells in area MSTd of the rhesus monkey that prefer optic flow signals containing speed gradient information the first step in determining the role of this area in signalling the speed of self motion or the three-dimensional structure of the environment has been taken. Speed gradient potentially provides two types of information. One type is related to changes in the speed of self motion and the second type is related to a change in the arrangement and relative distances of objects in the environment. Cells sensitive to speed gradients can therefore provide the subject with either one or both types of information. In order to determine the exact role of these cells, it is important to take further steps in testing speed gradient sensitive MSTd cells. Two types of hypothetical cells that may disambiguate the above two situations has been proposed. It should be mentioned

that assigning the task of the signalling of multidimensional information such as the speed of self-motion and the structure of the environment to single cell units is perhaps less likely. Signalling of this type of information is possibly the function of neuronal populations. And perhaps optic flow patterns of such may be analyzed by two different and coexisting single unit and population coding strategies.

It is hoped that the study outlined in this thesis has provided the first evidence of neuronal units that may play a role in the analysis of speed gradient information by our visual system.

ACKNOWLEDGEMENTS

I hope that in the past I have been able to reciprocate the attention and friendship and express my thanks to the following people for their support. I would like to take this opportunity to do so again. Many thanks to:

J.P. Roy for giving me the opportunity to work at the M.N.I., for your encouragement of creativity and independence, for your courage, and most importantly for your friendship. **Drs. Baker, Petrides,** and **Sadikot** for your academic input and your time. Professors from 204-526A, 555-500B, 531-630A, and 531-631B for opening so many windows. **Nahid, Guity, Dara, Dian,** and **Sara** for your unconditional love and support. **Ladan** for always caring and your good sense. **Duane, Jishnu, Katy, Lori, Onil,** and **Steve** for listening, for your patience, and your special friendships. **Lisa Volume** for your technical and moral support but most importantly for your sense of humour. **Ahmed, Clayton, Julia, Michel, Roger,** and **Zvi** for the endless discussions, your open-mindedness, and your advice on so many occasions. **Armando, Hiroto, Huai, Michaela, Valeri, Vesna,** and the many other friends on the 7th floor for sharing your ideas and experiences. **Mike Mazza** and **Mark Wolforth** for saving and re-saving my experiments and Thesis from being lost to the occasional (in my case not-so-occasional) mishaps of computers and technology. **Nadeem Ghani** and **Lynn Ziegler** for your answers to my never ending questions. **Janette, Bob, Danny, Jamal,** and **Matt** for your technical help and special kindness. **Monique Ledermann** for your help from day one. **Sandra Ironmonger** and **Victor Epp** for your secretarial assistance. **André** and those who helped me in the translation of parts of this work for your time.

And many thanks to all friends and individuals at the M.N.I. & H., from past and present, who helped create this unique institution and who continue to keep it at its best.

This work was financially supported by a grant from the Howard Hughes Medical Institute.

REFERENCE LIST

Baizer J.S., Ungerleider L.G., and Desimone R.. *Organization of visual inputs to the inferior temporal and posterior parietal cortex in macaques.* The Journal of Neuroscience 11(1): 168-190, 1991.

Berthoz A., Pavard B., and Young L.R.. *Perception of linear horizontal self-motion induced by peripheral vision (linearvection). Basic characteristics and visual-vestibular interactions.* Experimental Brain Research 23: 471-489, 1975.

Boussaoud D., Ungerleider L.G., and Desimone R.. *Pathways for motion analysis: cortical connections of the medial superior temporal and fundus of the superior temporal visual areas in the macaque.* The Journal of Comparative Neurology 296: 462-495, 1990.

Braunstein M.L., and Andersen G.J.. *Velocity gradients and relative depth perception.* Perception and Psychophysics 29(2): 145-155, 1981.

Braunstein M.L., and Tittle J.S.. *The observer-relative velocity field as the basis for effective motion parallax.* Journal of Experimental Psychology: Human Perception and Performance 14(4): 582-590, 1988.

Britten K.H., Shadlen M.N., Newsome W.T., and Movshon J.A.. *The analysis of visual motion: a comparison of neuronal and psychophysical performance.* The Journal of Neuroscience 12(12): 4745-4765, 1992.

Cavanagh P.. *Attention-based motion perception.* Science 257: 1563-1565, 1992.

Celebrini S., and Newsome W.T.. *Neuronal and psychophysical sensitivity to*

motion signals in extrastriate area MST of the macaque monkey. The Journal of Neuroscience 14(7): 4109-4124, 1994.

De Yoe E.A., and Van Essen D.C.. *Concurrent processing streams in monkey visual cortex.* Trends in Neuroscience 11(5): 219-226. 1988.

Desimone R., and Ungerleider L.G.. *Multiple visual areas in the caudal superior temporal sulcus of the macaque.* The Journal of Comparative Neurology 284: 164-189, 1986.

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

Felleman D.J., and Van Essen D.C.. *Distributed hierarchical processing in the primate cerebral cortex.* Cerebral Cortex 1(1): 1-47, 1991.

Ferris S.H.. *Motion parallax and absolute distance.* Journal of Experimental Psychology 95(2): 258-263, 1972.

Gibson J.J.. *The perception of the visual world.* The Houghton Mifflin Company, Cambridge, pp. 117-144, 1950.

Graziano M.S.A., Andersen R.A., Snowden R.J.. *Tuning of MST neurons to spiral motions.* The Journal of Neuroscience 14(1): 54-67, 1994.

Harris M.G.. Optic and retinal flow. In: *Visual detection of motion* (Smith A.T., and Snowden R.J. eds.). Academic Press Limited, San Diego, pp. 307-332, 1994.

Koenderink J.J.. *Optic flow.* Vision Research 26(1): 161-180, 1986.

Komatsu H., and Wurtz R.H.. *Modulation of pursuit eye movements by stimulation of cortical areas MT and MST.* Journal of Neurophysiology 62(1): 31-47, 1989.

Lagae L., Maes H., Raiguel S., Xiao D.K., and Orban G.A.. *Responses of macaque STS neurons to optic flow components: a comparison of areas MT and MST.* Journal of Neurophysiology 71(5): 1597-1626, 1994.

Maunsell J.H., and Newsome W.T.. *Visual processing in monkey extrastriate cortex.* Annual Review of Neuroscience 10: 363-401, 1987.

Morrone M.C., Burr D.C, and Vaina L.M.. *Two stages of visual processing for radial and circular motion.* Nature 376: 507-509, 1995.

Nakayama K., and Loomis J.M.. *Optical velocity patterns, velocity-sensitive neurons, and space perception: a hypothesis.* Perception 3: 63-80, 1974.

Nakayama K.. *Biological image motion processing: a review.* Vision Research 25(5): 625-660. 1985.

Newsome W.T., and Paré E.B.. *A selective impairment of motion perception following lesions of the middle temporal visual area (MT).* The Journal of Neuroscience 8(6): 2201-2211, 1988.

Newsome W.T., and Salzman C.D.. *The neuronal basis of motion perception.* Experimental and theoretical studies of consciousness. Wiley, Chichester; Ciba Foundation Symposium 174: 217-246, 1993.

Ono M.E., Rivest J., and Ono H.. *Depth perception as a function of motion parallax and absolute-distance information.* Journal of Experimental Psychology 12(3): 331-337, 1986.

Pasternak T., and Merrigan W.H.. *Motion perception following lesions of the superior temporal sulcus in the monkey.* Cerebral Cortex 4: 247-259, 1994.

Rogers B., and Graham M.. *Motion parallax as an independent cue for depth perception.* Perception 8: 125-134, 1979.

Rogers S., and Rogers B.J.. *Visual and nonvisual information disambiguate surfaces specified by motion parallax.* Perception and Psychophysics 52(4): 446-452, 1992.

Roy J.P., and Wurtz R.H.. *The role of disparity-sensitive cortical neurons in signalling the direction of self-motion.* Nature 348(6297): 160-162, 1990.

Roy J.P., and Wurtz R.H.. *Disparity sensitivity of neurons in monkey extrastriate area MST.* The Journal of Neuroscience 12(7): 2478-2492, 1992.

Royden C.S., Banks M.S., and Crowell J.A.. *The perception of heading during eye movements.* Nature 360: 583-585, 1992.

Saito H., Yukie M., Tanaka K., Hikosaka K., Fukada Y., and Iwai E.. *Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey.* The Journal of Neuroscience 6(1): 145-157, 1986.

Salzman C.D., Britten K.H., and Newsome W.T.. *Cortical microstimulation influences perceptual judgements of motion direction.* Nature 346: 174-177, 1990.

Southall J.P.C. ed.. *Helmholtz's treatise on physiological optics*, Volume III. George Banta Publishing Company, Wisconsin, 1925.

Tanaka K., and Saito H.. *Analysis 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 62(3): 626-641, 1989.

Van Den Berg A.V.. *Robustness of perception of heading from optic flow.* Vision Research 32(7): 1285-1296, 1992.

Van Essen D.C., and Maunsell J.H.R.. *Hierarchical organization and functional streams in the visual cortex.* Trends in Neuroscience 6: 370-375, 1983.

Warren W.H., and Hannon D.J.. *Direction of self-motion is perceived from optical flow.* Nature 336:162-163, 1988.

Warren W.H., Morris M.W., and Kalish M.. *Perception of translation heading from optic flow.* Journal of Experimental Psychology: Human Perception and Performance 14(4): 646-660, 1988.

Wurtz R.H., Yamasaki D.S., Duffy C.J., and Roy J.P.. *Functional specialization for visual motion processing in primate cerebral cortex.* Cold Spring Harbor Symposia on Quantitative Biology, Vol. LV: 717-727, 1990.

Wurtz R.H., Duffy C.J, and Roy J.P.. Motion processing for guiding self-motion. In : *Brain mechanisms of perception and memory: from neuron to behaviour* (Ono T., Squire L.R., Raichle M.E., Perret D., and Fukuda M. eds.). Oxford University Press, New York, 1993.

Zihl J., Von Cramon D., and Mai N.. *Selective disturbance of movement vision after bilateral brain damage.* Brain 106: 313-340, 1983.