

Neuronal Mechanisms of Actively Steering Optic Flow: Global versus Local Motion

Zarina Ali, 2004

Advised by Dr. Charles Duffy, M.D., Ph.D.

Department of Neurobiology and Anatomy

Optic flow provides a moving observer with information about heading and the 3-dimensional layout of the environment. Passive viewing of optic flow by a passenger is a very different experience than active steering of optic flow by a driver, although the same optic flow fields are seen. The driver would seem to be more engaged in visual motion processing in order to actively steer the heading direction, as compared to the passenger. In addition, optic flow might be analyzed by perceiving the global pattern of motion or by responding to a local patch of motion in the pattern. Medial superior temporal (MST) neurons show optic flow selective responses with tuning for the simulated heading of observer self-movement.¹ We have now compared MST neuronal responses to optic flow during global and local motion processing of passive viewing and active steering of the simulated heading direction of optic flow.

The data suggest that MST neuronal responses to optic flow are influenced by tasks that require real-time visual analysis. Passive and active observers both process optic flow, but their responses to those stimuli differ. Top-down mechanisms may enhance MST responses when the subject uses global motion and actively suppress responses when using local motion strategies. These motion strategies may be particularly relevant when local and global motion are incongruent, such as tracking the path of a deer as it crosses one's path.

The results indicate that most MST neurons respond differently to optic flow during passive and active conditions when the monkey uses global motion. The most robust effects are the enhancement of MST responses in the active steering condition and the suppression of MST response in the passive viewing condition. In addition, we speculate that the use of a local motion strategy to process optic flow tends to suppress MST, while a global motion strategy enhances MST response. This response suppression (local) and enhancement (global) is not limited to the preferred stimulus direction and is evident under both passive and active steering conditions.

Optic Flow Perception

In 1950, J.J. Gibson coined the term "optic flow" to refer to the patterned visual motion by a moving observer.² Gibson studied how observers estimate their position and orientation in space, suggesting that optic flow provides the observer with information about his movement and the 3-dimensional layout of his environment to guide self-movement. In his schematic illustration of optic flow (Figure 1), he depicted the optic flow seen by a pilot trying to land a plane on a landing strip. As the plane moves forward, stationary objects are seen to move radially with increasing speeds towards the peripheral visual field. The center of this expanding radial pattern is called the focus of expansion (FOE) and indicates the observer's heading direction.

Figure 2 shows the overhead view of the observer's movement (left panels) and the retinal pattern of optic flow (right panels). If the observer moves forward while looking straight ahead (A, left), a radial pattern of optic flow (arrows) is projected onto the retina and the FOE indicates the direction of the observer's movement (A, right). When the observer moves right-forward (B, left), the observer sees a radial pattern in which the focus of expansion is displaced to the right of gaze, indicating a rightward heading direction.³

Studies have shown that in order to guide ordinary locomotive activities like skiing or running, one must estimate heading within 1-3 degrees.⁴ Other findings have indicated that observers judge their heading with great accuracy; thresholds are at least as low as 0.5 degrees when viewing optic flow.^{5,6} The length of exposure to the optic flow seems to be important also, as performance improves with increased viewing times of optic flow.⁷

Smooth pursuit eye movements made in order to track objects during self-movement add to the optic flow image, resulting in an FOE that is shifted towards the direction of eye movement. Therefore, during pursuit, heading estimation from optic flow is more complicated.⁸ Psychophysical studies have indicated that humans can

still estimate their direction of heading from the resulting retinal motion, although this heading estimation during pursuit improves with the addition of multiple depth planes in optic flow.⁹⁻¹¹

Recent studies have shed light on the neural mechanisms of optic flow perception. In particular, studies have shown that when an observer is presented with a random dot display, his sensitivity to the direction of motion enhances as the area of the display increases. This psychophysical result provides further evidence for spatial integration and summation of optic flow over large regions of space within the visual system. In addition, the sensitivity to the motion of optic flow seems to be sharply tuned for speed, which is consistent with the physiology of MST neurons.¹² Duffy and Wurtz have proposed that this sharp tuning for speed allows for the integration across multiple depth planes during combined self-movement and pursuit.¹²

Optic Flow Neurophysiology

MST is categorized into two distinct regions: lateral (MSTl) and dorsal (MSTd).^{13,14} In general, MSTl neurons have smaller receptive fields than MSTd cells. Some MSTl neurons are suited for discriminating a moving object from the background because they exhibit center-surround disparity selectivity. MSTd neurons have very large receptive fields; many neurons respond to stimuli within a full quadrant or a complete hemi field.^{13,15-17}

Saito et al. used anesthetized and paralyzed monkeys to study the visual response properties of neurons in the cortical area surrounding the middle temporal area (MT) in the superior temporal sulcus (STS).¹⁴ Their findings indicate a functionally distinct region where three classes of directionally-selective cells with large receptive fields cluster: MSTd. One class of cells responded to a straight movement of patterns in the fronto-parallel plane with directional selectivity (51.4%), the second class of cells selectively responded to an expanding or contracting size-change of patterns (15.7%), and the third class of cells responded only to a rotation of patterns in one direction (13.7%). They suggested that these cells integrate motion information extracted by MT cells.

Duffy and Wurtz suggested that the selective responses of many MSTd neurons to the rotational and translational components of optic flow deemed them important in contributing to the analysis of optic flow fields.¹⁸ When they investigated whether neurons that respond to radial and circular motion respond differently when the center of motion was shifted to different regions of the visual field,¹ they found that about 90% of the neurons studied responded differently when the center of motion was shifted away from the center of the field. In addition to showing selective responses to simulated heading direction in optic flow, these MSTd neurons also displayed sensitivity to speed gradients.¹² In addition, Bradley et al. demonstrated that MSTd neurons have different FOE preferences for optic flow presented during fixation and pursuit.¹⁹ Overall, MSTd neurons are assumed to respond to movement of the observer, which is important in navigation and spatial orientation.²⁰

Lesion studies help confirm MT and MST's role in

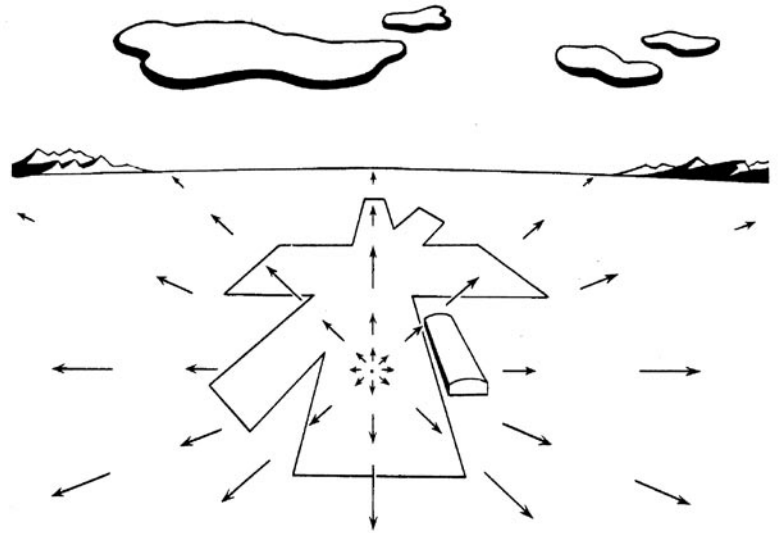


Figure 1: Gibson's Depiction of Optic Flow: This schematic illustration depicts images of objects and their motion patterns seen by a pilot during runway approach. As the plane approaches, objects appear to radiate outwards from the heading direction, called the focus of expansion (FOE). The radial speeds of the objects increase as they move from the FOE, depending on the distance to the observer. The location of the FOE could be used to navigate a successful landing.

motion perception. Chemical lesions made to area MT in conjunction with psychophysical tasks were used to assess sensitivity to motion. Results indicated that the lesions into MT caused striking elevations in motion thresholds, suggesting that neural activity in MT contributes selectively to the perception of motion.²¹ Bilateral lesions of areas MT/MST of varying intensity caused a temporary disruption, followed by at least partial recovery, of most motion thresholds. Permanent effects of the lesions on visual sensitivity were graded with lesion extent. In general, these results demonstrated that MT/MST areas make an important contribution to the performance of various motion perception tasks including the discrimination of differences in direction and speed, and the perception of global motion in the presence of directional noise.²²

Salzman et al. tested the effects of cortical microstimulation on perceptual judgements of motion direction on rhesus monkeys.²³ They determined that microstimulation biases the monkey's behavior in a direction that is predicted by the neuron near the stimulating electrode. This demonstrates a functional link between the activity of direction-selective neurons and perceptual judgements of motion direction.²³ Celebrini and Newsome electrically stimulated clusters of directionally selective neurons in MST in Rhesus monkeys during a direction discrimination task and found that microstimulation biased the monkeys' choices toward the direction of motion encoded by MST neurons at the stimulation site.²⁴ Since receptive fields in MST are typically much larger than those in MT, Celebrini and Newsome determined that stimulation of a single site in MST can influence judgements over a much larger portion of the visual field than equivalent stimulation in MT.²⁴

Britten and van Wezel tested the hypothesis that MST is involved in the analysis of self-motion by electrically microstimulating MST while monkeys performed a visual heading discrimination task.²⁵ They found that

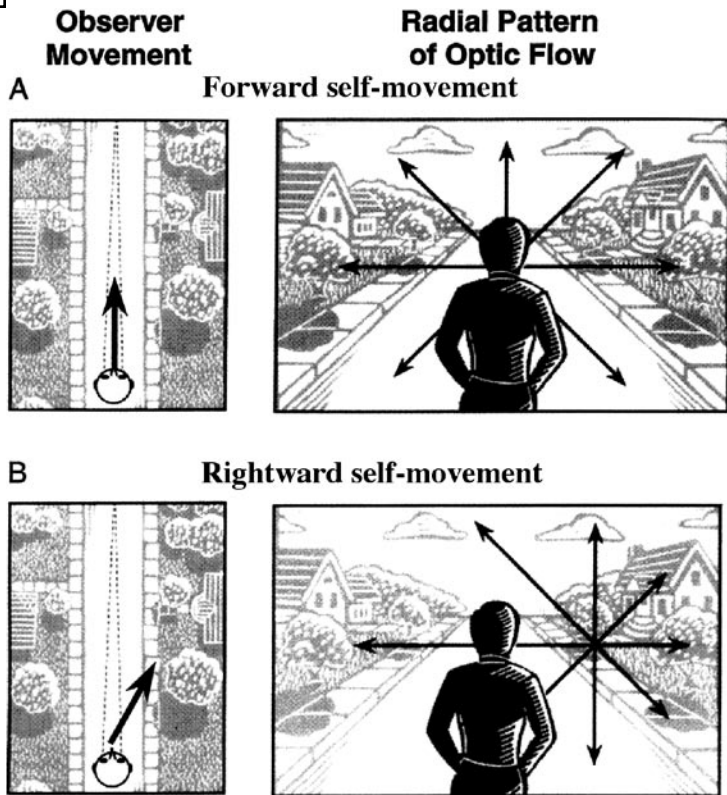


Figure 2: Overhead view of the observer's movement (left panels) and the optic flow (right panels). If the observer moves forward while looking straight ahead (A, left), a radial pattern of optic flow (arrows) is projected onto the retina and the FOE indicates the direction of the observer's movement (A, right). When the observer moves right-forward (B, left), the observer sees a radial pattern in which the focus of expansion is displaced to the right of gaze, indicating a rightward heading direction. (Adapted from Duffy et al., 2003)

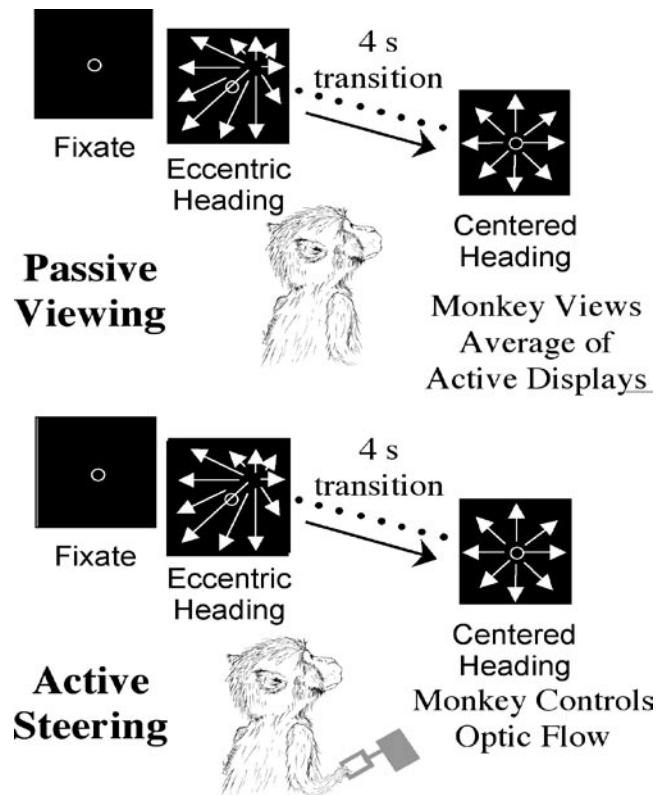


Figure 3: The monkey maintained centered fixation while the heading in optic flow changed from one of 8 eccentric directions to the straight-ahead centered heading.

Passive Viewing: The monkey did not touch the joystick while the heading in optic flow transitioned toward the center.

Active Steering: The monkey used the joystick to actively steer the heading to the centered heading direction.

in a majority of the experiments, microstimulation induced a significant bias in the monkey's decision. This result suggests that MST signals representing heading are used by the monkey in forming heading judgments.²⁵

More recently, Eskandar and Assad examined neuronal signals in the monkey area MST during visually guided hand movements and tested whether the direction selectivity depended on the direction of the stimulus spot or the direction of the hand movement.²⁶ They trained animals to use a joystick to guide a spot to a target and found that many neurons responded in a direction-selective manner in this guidance task. One of the tasks involved recording the movement of the spot while the monkey actively steered it, and then playing back that movement in a passive trial during fixation.

Their results indicated that MST neurons were active and directional in both joystick-movement mode and playback mode and were not affected by the direction of hand movement.

Overview of Thesis

The present study attempts to address MST neuronal responses to optic flow viewed passively or during the active steering of the stimulated heading direction. We hypothesize that MST neuronal responses will be inhibited during passive trials and enhanced during active trials. During the active trial, we assume that MST neurons are actively engaged in the global motion perception and steering of the simulated heading direction, while in the passive trial, MST neurons are not as responsive to the heading direction.

In experiment 1, we analyzed MST neuronal responses from

passive movement of heading in optic flow from one of eight eccentric directions to the straight-ahead centered heading, while the monkey maintained centered fixation. We compared this to MST neuronal responses during active steering, in which the monkey used a joystick to actively steer the heading to the centered heading direction, while also maintaining fixation.

Experiment 2 was identical to Experiment 1, except that a total of sixteen optic flow stimuli were used, eight outward and eight inward radial patterns requiring the monkey to use global motion processing of the entire scene rather than local processing at the center of the screen. Again, we compared MST neuronal responses during active steering and passive fixation.

Experiment 1: Local Motion

Dot motion in the optic flow presented in Experiment 1 simulated the observer's movement with respect to a remote fronto-parallel surface as an outward radial pattern emanating from a focus of expansion (FOE). Eight optic flow stimuli were used that contained FOEs displaced 20° from the center, and distributed at 45° intervals around 360°. During active steering trials, the monkey's task was to use the joystick to actively steer the heading of the optic flow to the centered heading direction (Figure 3). During passive trials, the displaced FOE moved in a straight line to the center. These passive optic flow stimuli were averages of active displays. Active and passive trials consisted of eight conditions that were randomly interleaved within altering blocks of either active or passive trials. Four to six trials for each condition were successfully completed for each recording session.

Most MST neurons responded differently to optic flow during passive and active conditions. The most robust effects were the suppression of activity in the active steering condition. In some directionally selective neurons, this effect was seen in the absence of a change in directionality of the neuron, suggesting a general increase in response for the preferred heading during active steering compared to passive viewing.

In other neurons, active steering influenced the strength of directional responses by changes in response amplitudes, despite the overall decrease in activity during active trials. This suggests that the increased responses in the passive condition cause neurons to lose their directional sensitivity as a generally high firing rate is observed for all heading directions.

In the population sample of MST neurons, preferred heading and heading selectivity did not seem to change with passive viewing or active steering. However, many MST neurons showed an increased strength of directional responses and peak responses during passive viewing, as

compared to active steering. These findings led us to consider whether the monkey might be using local motion cues to steer the FOE. This speculation is consistent with our findings, but it is not obvious why this should suppress MST neuronal activity as local motion processing might proceed very well without suppressing MST.

Experiment 2: Global Motion

Optic flow stimuli and behavioral tasks in Experiment 2 were the same as that of Experiment 1 except that eight inward radial optic flow patterns were added to the stimulus set (Figure 4). These simulated the movement of the observer away from a remote fronto-parallel surface with dot motion inward toward the focus of contraction (FOC). Passive playback was identical to previous active trial for each optic flow pattern. Active and passive trials were block-wise interleaved and four to six trials of each condition were successfully completed for each recording session.

We proposed the local motion hypothesis about the monkey's perceptual strategy in Experiment 1. This is based on the view that optic flow might be analyzed either by perceiving the global pattern of motion or by responding to a local patch of motion in the pattern. We speculate that MST might be suppressed during active steering if the monkey is using a local motion strategy, rather than processing the global pattern of optic flow.

Training with in/out optic flow promoted the monkey's use of the global pattern rather than the use of ambiguous local motion cues during active steering. Contrary to results obtained from Experiment 1, some MST neurons showed a robust enhancement of neuronal activity in the active steering condition in Experiment 2. In addition, response enhancement (global) and suppression (local) was not limited to the preferred heading direction. These results supported our hypothesis that MST neuronal activity would increase during active steering of a simulated

optic flow heading, as compared to passive viewing of the optic flow.

MST, Navigation, and Spatial Orientation

Passive and active observers both process optic flow, but their responses to those stimuli often differ. Given the change of responses in MST neurons during simulated optic flow heading in passive viewing and active steering conditions, we find that MST neuronal responses to optic flow are influenced by tasks that require real-time visual analysis.

In particular, active steering by global motion enhances MST's optic flow responses. We suggest that top-down mechanisms may enhance MST responses when the subject uses global motion and actively suppress responses when using local motion strategies. We believe that a local motion strategy may be better served by MT's smaller, more central, direction selective receptive fields. These differences in motion strategies may be particularly relevant when the local and global motion are incongruent. This may be important when tracking the motion of an object as it crosses one's path.

MSTd's Role in Papez's Circuit for Navigation and Orientation

Movement through the environment is accompanied by a diverse array of sensory cues about observer direction and speed. MSTd neurons combine visual and vestibular cues about self-movement with oculomotor signals about pursuit eye movements to create a wide variety of response properties. The population response in MSTd estimates the direction of observer self-movement with greater accuracy in light than in darkness and without significant detrimental effects of concurrent pursuit eye movements.

As previous studies have shown, MSTd neurons are involved in determining self-movement direction. However, they also show selectivity for particular paths. In addition, some MSTd neurons show place specific responses both during translational

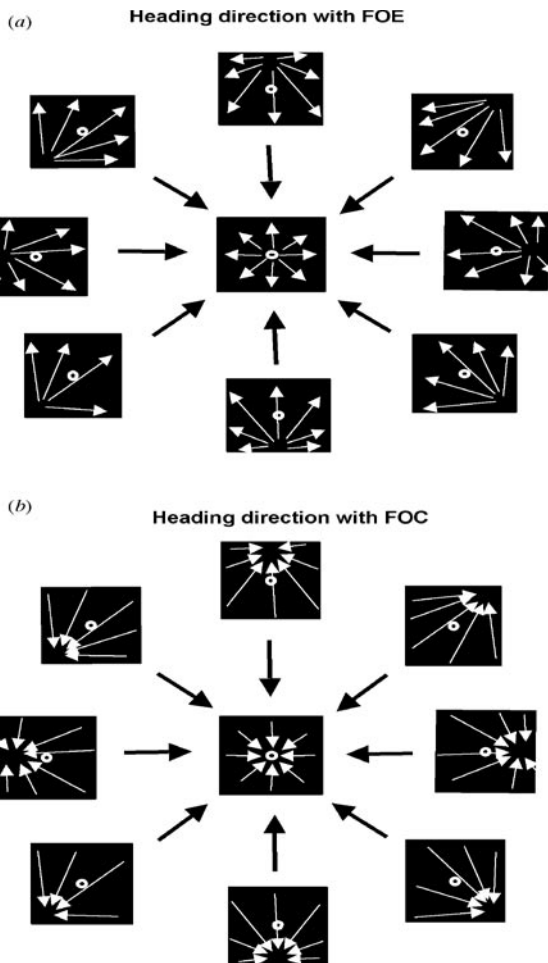


Figure 4: Optic flow stimuli with heading direction indicated by FOE (a) and FOC (b): (a) Optic flow simulates the observer's movement with respect to a remote fronto-parallel surface as an outward radial pattern emanating from a focus of expansion (FOE), or (b) as an inward radial pattern emanating from a focus of contraction (FOC). Experiment 1 used only FOEs originating from one of eight eccentric directions, which the monkey passively viewed or actively steered to the centered heading while experiment 2 used both FOEs and FOCs in the same task.

movement and when the animal is held at a stationary position in the room.²⁷ Thus, MSTd neurons are capable of integrating sensory and oculomotor information to represent self-movement, guide locomotion, and contribute to spatial orientation. Recently, Duffy et al. suggested that the posterior parietal cortex may be engaged in a navigational circuit with reciprocal interactions with hippocampal, thalamic, and other cortical centers that create a cortical-subcortical system that is parallel to Papez's emotional circuit but is devoted to information processing for navigation and spatial orientation.²⁸

They propose that Papez's circuit

for navigation might be thought of as beginning in dorsal extrastriate visual cortical areas that combine visual, vestibular, and other signals relevant to self-movement perception and to spatial orientation.²⁹⁻³¹ These parieto-temporal areas are reciprocally connected with parahippocampal cortices³²⁻³⁸ that then connect reciprocally with the hippocampus.³⁹⁻⁴³ The place neuron responses in the hippocampus might be the result of spatial activity in the hippocampus.⁴⁴⁻⁴⁶

Parahippocampal and subicular areas project to the anterior and lateral dorsal thalamus via the fornix and the mammillo-thalamic tract.⁴⁷ These connections may contribute to head direction sensitivity. Reciprocal projections from the anterior and lateral dorsal thalamus to posterior cingulate and retrosplenial cortical areas⁴⁸⁻⁵⁰ engage these cortical areas in spatial processing.⁵¹ These projections then connect reciprocally to posterior parietal cortical areas, completing the cortico-subcortical circuit.^{48,50,53,54} Thus, Duffy et al. proposes a "bidirectional information flow supporting navigation and spatial orientation."²³

Thus, the involvement of cortical and subcortical systems allows for the integration of memory and motivation to influence MST neuronal responses. In particular, MSTd's engagement in reciprocal interactions with hippocampal, thalamic, and other cortical centers creates a system that is parallel to Papez's emotional circuit for information processing. With the influence of memory and motivation from this cortical-subcortical system, MSTd neurons integrate sensory and oculomotor information for navigation and spatial orientation.

1. Duffy C. J. and Wurtz R. H. Response of monkey MST neurons to optic flow stimuli with shifted centers of motion. *J. Neuroscience* 15: 5192-5208, 1995.

2. Gibson J. J. *The Perception of the Visual World*. Houghton Mifflin, Boston, 1950.

3. Hamed S., Page W.K., Duffy C.J., and Pouget, A. MSTd neuronal basis functions for the population encoding of heading direction. *Journal of Neurophysiology*, 2003.

4. Cutting J. E., Springer K., Braren P. A. and Johnson S. H. Wayfinding on foot from information in retinal, not optical, flow. *J. Exp. Psych. : General* 41-72, 1992.

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

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

7. Crowell J. A., Royden C. S., Banks M. S., Swenson K. H. and Sekular A. B. Optic flow and heading judgements. *Investigative Ophthalmology & Visual Science. Suppl.* 31:522,1990.

8. Longuet-Higgins, H. C. and Prazdny K. The interpretation of a moving retinal image. *Proc. R. Soc. Lond. B* 208: 385-397, 1980.

9. Warren W. H., Jr. and Hannon D. J. Eye movements and optical flow. *Journal of the Optical Society of America A-Optics & Image Science* 7: 160-169, 1990.

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

11. Stone L. S. and Perrone J. A. Human Heading Estimation During Visually Simulated Curvilinear Motion. *Vision Research* 37: 573-590, 1997.

12. Duffy C. J. and Wurtz R. H. Medial Superior Temporal Area Neurons Respond to Speed Patterns in Optic Flow. *J. Neuroscience* 17: 2839-2851, 1997.

13. Desimone R. and Ungerleider L. G. Multiple visual areas in the caudal superior temporal sulcus of the macaque. *J. Comp. Neurol.* 248: 164-189, 1986.

14. 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. *J. Neuroscience* 6:145-157, 1986.

15. Van Essen D. C., Maunsell J. H. R. and Bixby J. L. The middle temporal visual area in the macaque: Myeloarchitecture, connections, functional properties and topographic representation. *J.Comp. Neurol.* 199: 293-326, 1981.

16. Tanaka K., Hikosaka K., Saito H., Yukie M., Fukada Y. and Iwai E. Analysis of local and wide-field movements in the superior temporal visual areas of the macaque monkey. *J. Neuroscience* 6:134-144, 1986.

17. Komatsu H. and Wurtz R. H. Relation of cortical areas MT and MST to pursuit eye movements. I. Localization and visual properties of neurons. *J. Neurophysiology* 60(2): 580-603, 1988.

18. Duffy C. J. and Wurtz R. H. Sensitivity of MST neurons to optic flow stimuli. *J. Neurophysiology* 65: 1329-1359, 1991.
19. Bradley D. C., Maxwell M., Andersen R. A., Banks M. S., Shenoy K. V. Mechanisms of Heading Perception in Primate Visual Cortex. *Science* 273: 1544-1549, 1996.
20. Eifuku S. and R. H. Wurtz. Response to motion in extrastriate area MSTl: center-surround interactions. *J. Neurophysiology* 80:282-296, 1998.
21. Newsome W. T. and Pare E. B. A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *J. Neuroscience* 8(6):2201-2011, 1988.
22. Pasternak T. and Merigan W. H. Motion perception following lesions of the superior temporal sulcus in the monkey. *Cerebral Cortex* 4:247-259, 1994.
23. Salzman C. M., Murasugi C. M., Britten K. H. and Newsome W. T. Microstimulation in visual area MT: effects of direction discrimination. *J. Neuroscience* 12(6):2331-2355, 1992.
24. Celebrini S. and Newsome, W.T. Neuronal and psychophysical sensitivity to motion signals in extrastriate area MST of the macaque monkey. *J. Neuroscience* 14:4109-4124, 1994.
25. Britten K. H. and van Wezel, R. J. A. Electrical microstimulation of cortical area MST biases heading perception in monkeys. *Nature Neuroscience* 1:59-63, 1998.
26. Eskandar E. N. and Assad J. Distinct nature of directional signals among parietal cortical areas during visual guidance. *J. Neurophysiology* 88:1777-1790, 2002.
27. Froehler M.T. and Duffy C.J. Cortical Neurons Encoding Path and Place: Where You Go is Where You Are. *Science* 295: 2462-2465, 2002.
28. Duffy C. J., Page W. K. and Froehler M. T. Posterior Cortical Processing of Self-movement Cues: MSTd's role in Papez's circuit for navigation and orientation, 2004.
29. Schaafsma S. J. and Duysens J. Neurons in the Ventral Intraparietal Area of Awake Macaque Monkey Closely Resemble Neurons in the Dorsal Part of the Medial Superior Temporal Area in Their Responses to Optic Flow. *J. Neurophysiol.* 76: 4056-4068, 1996.
30. Siegel, R. M. and Read, H. L. Analysis of Optic Flow in the monkey Parietal Area 7a. *Cerebral Cortex* 7: 327-346, 1997.
31. Bremner, F., Duhamel, J. R., Ben, H., and Graf, W. Heading encoding in the macaque ventral intraparietal area (VIP). *European Journal of Neuroscience.* 16: 1554-1568, 2002.
32. Jones E. G., Powell T. P. S. An Anatomical Study of Converging Sensory Pathways Within the Cerebral Cortex of the Monkey. *Brain* 93: 793-820, 1970.
33. Van Hoesen, G. W. The Parahippocampal Gyrus: New observations Regarding Cortical Connections in the Monkey. *Trends in Neurosciences* 5: 345-350, 1982.
34. Kosel, K. C., Van, H., and Rosene, D. L. Non-hippocampal cortical projections from the entorhinal cortex in the rat and rhesus monkey. *Brain Research* 244: 201-213, 1982.
35. Anderson, R. A., Asanuma, C., Essick, G., and Siegel, R. M. Corticocortical connections of anatomically and physiologically defined subdivisions within the inferior parietal lobule. *Journal of Comparative Neurology* 296: 65-113, 1990.
36. Clower, D. M., West, R. A., Lynch, J. C., and Strick, P. L. The inferior parietal lobule is the target of output from the superior colliculus, hippocampus, and cerebellum. *Journal of Neuroscience* 21: 6283-6291, 2001.
37. Lavenex, P., Suzuki, W. A., and Amaral, D. G. Perirhinal and 999parahippocampal cortices of the macaque monkey: projections to the neocortex. *J. Comp. Neurol.* 447: 394-420, 2002.
38. Ding, S. L., Morecraft, R. J., and Van, H. Topography, cytoarchitecture, and cellular phenotypes of cortical areas that form the cingulo-parahippocampal isthmus and adjoining retrosplenial areas in the monkey. *J. Comp. Neurol.* 456: 184-201, 2003.
39. Mesulam M. M., Van Hoesen G. W., Pandya D. N. and Geschwind N. Limbic and sensory connections of the inferior parietal lobule (area PG) in the rhesus monkey: a study with a new method for horseradish peroxidase histochemistry. *Brain Res.* 136(3): 393-414, 1977.
40. Rosene, D. L. and Van, H. Hippocampal efferents reach widespread areas of cerebral cortex and amygdala in the rhesus monkey. *Science.* 198: 315-317, 1977.
41. Amaral, D. G., Insausti, R., and Cowan, W. M. Evidence for a direct projection from the superior temporal gyrus to the entorhinal cortex in the monkey. *Brain Research* 275: 263-277, 1983.
42. Cavada, C. and Goldman-Rakic, P. S. Posterior parietal cortex in rhesus monkey: I. Parcellation of areas based on distinctive limbic and sensory corticocortical connections. *J. Compar. Neurol.* 287: 393-421, 1989.
43. Rockland, K. S. and Van Hoesen, G. W. Some Temporal and Parietal Cortical Connections Converge in CA1 of the Primate Hippocampus. *Cerebral Cortex* 9: 232-237, 1999.
44. O'Keefe, J. and Nadel, L. *The Hippocampus as a Cognitive Map.* UK, Clarendon, Oxford. 1978.
45. McNaughton, B. L., Mizumori, S. J. Y., Barnes, C. A., Leonard, B. J., Marquis, M., and Green, E. J. Cortical Representation of Motion During Unrestrained Spatial Navigation in the Rat. *Cerebral Cortex* 4: 27-39, 1994.
46. Nishijo, H., Ono, T., Eifuku, S., and Tamura, R. The Relationship between Monkey Hippocampus Place-Related Neural Activity and Action in Space. *Neurosci.Letters* 226: 57-60, 1997.
47. Aggleton, J. P., Desimone, R., and Mishkin, M. The origin, course, and termination of the hippocampothalamic projections in the macaque. *J. Compar. Neurol.* 243: 409-421, 1986.
48. Baleyrier, C. and Mauguier, F. The duality of the cingulate gyrus in monkey. Neuroanatomical study and functional hypothesis. *Brain.* 103: 525-554, 1980.
49. Mufson, E. J. and Pandya, D. N. Some observations on the course and composition of the cingulum bundle in the rhesus monkey. *J. Compar. Neurol.* 225: 31-43, 1984.
50. Morris, R., Petrides, M., and Pandya, D. N. Architecture and connections of retrosplenial area 30 in the rhesus monkey (*Macaca mulatta*). *European Journal of Neuroscience* 11: 2506-2518, 1999.
51. Whishaw, I. Q., Maaswinkel, H., Gonzalez, C. L., and Kolb, B. Deficits in allothetic and idiothetic spatial behavior in rats with posterior cingulate cortex lesions. *Behavioral Brain Research.* 118: 67-76, 2001.
52. Pandya, D. N., Van, H., and Mesulam, M. M. Efferent connections of the cingulate gyrus in the rhesus monkey. *Experimental Brain Research.* 42: 319-330, 1981.
53. Leichnetz, G. R. Connections of the medial posterior parietal cortex (area 7m) in the monkey. *The Anatomical Record* 263: 215-236, 2001.

Zarina Ali graduated in Spring 2004 with a B.S. Degree with Distinction in Research in Neuroscience. This article is an abridged version of her senior honors thesis. Zarina is currently pursuing a joint M.D.-M.B.A. degree at the University of Rochester School of Medicine and the William E. Simon Graduate School of Business Administration.