

Optic flow: A brain region devoted to optic flow analysis?

Robert H. Wurtz

The visual motion – or optic flow – that results from an observer's own movement can indicate the direction of heading through the environment. Recent experiments have strengthened the argument that neurons in a specialized region of the cerebral cortex are critical for the analysis of this important class of visual stimuli.

Address: Laboratory of Sensorimotor Research, National Eye Institute, National Institutes of Health, Bethesda, Maryland, 20892-4435, USA.

Current Biology 1998, 8:R554–R556
<http://biomednet.com/elecref/09609822008R0554>

© Current Biology Publications ISSN 0960-9822

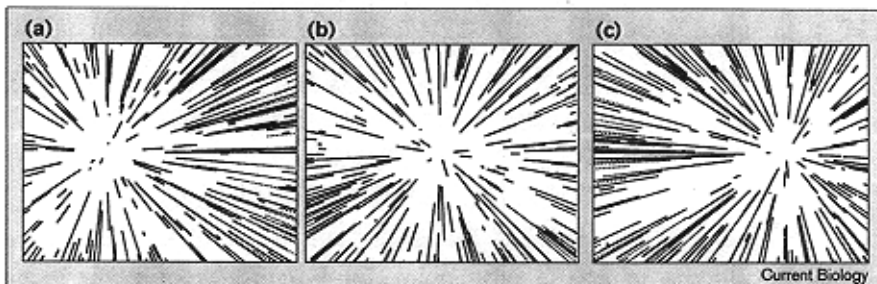
Optic flow is the visual motion that results from an observer's own movement through the environment. The distinguishing feature of optic flow is that it covers the entire visual field, whereas object motion covers only a part of the field. Nearly 50 years ago, the American experimental psychologist James J. Gibson [1] emphasized that the changes in the optic flow pattern over time are critical for indicating the direction in which the observer is moving or 'heading', while also providing cues about the structure of the environment — near objects will move faster than more distant objects — and for the control of posture — side-to-side patterns induce body sway. Particularly relevant, in light of recent work, was Gibson's description of how the radial expansion of the visual scene could be taken to indicate the direction of heading (Figure 1). Gibson and others [2,3] suggested that, even when this radial flow is combined with other motion, such as that produced by eye movements, optic flow can be used to determine the direction of heading. These behavioral studies of optic flow raised the tantalizing question of what neuronal mechanisms might support such large-field visual analysis.

At the time Gibson was putting forward his then unconventional views, the way visual information is processed along the visual pathways from the retina to the striate cortex, or visual area V1, was being explored [4]. The processing of visual motion that was observed in those early studies would be appropriate for the analysis of movement over only a tiny portion of the visual field, because of the small size of the cell's receptive fields; optic flow patterns, however, cover the entire visual field. The breakthrough in this mismatch came with two developments. The first was the identification of a series of cerebral cortical areas devoted to visual processing that lie in front of the striate cortex (Figure 2). The second was the recognition that several of these areas are devoted to visual motion processing. In one of these extra-striate areas, the middle temporal area (MT or V5), there was still a mismatch between the receptive field sizes and optic flow requirements; even though the receptive fields of MT cells are roughly ten times the size of those in striate cortex, they still cover only a relatively small fraction of the visual field. But when an adjacent motion area, the medial superior temporal area (MST), was investigated, its neurons were found to be directionally selective with receptive fields that cover large parts of the visual field [5,6].

But do MST neurons respond to the types of motion included in optic flow? Following the initial reports that some MST neurons respond to looming (expanding) and to rotating stimuli [7], they were shown to respond to large field optic flow stimuli such as those illustrated in Figure 1a [8–12]. Additional characteristics of the neurons made them particularly good candidates for involvement in the analysis of optic flow, and particularly in heading determination. These include their sensitivity to shifts in

Figure 1

Simulations of optic flow patterns that result from forward movement of the observer. The center panel (b) shows the symmetric pattern produced when the eyes and head are directed straight ahead and the observer is moving (heading) straight ahead. The direction of each line indicates the direction a particular point in the environment would take if it were followed over time (away from the central focus of expansion); the length of the line indicates the speed of the motion (longer lines indicate faster motion in the periphery). (a) When the observer continues to look straight ahead but is heading to the left, the focus of expansion is on the left. (c) When the observer looks straight ahead but heads to



the right, the focus of expansion is on the right. These examples represent only the simplest optic flow patterns; forward motion is frequently accompanied by a rotation of the

eyes and head so that the optic flow pattern falling on the retina is a combination of the radial motion and the rotary motion from the eyes and head. (Modified from [16].)

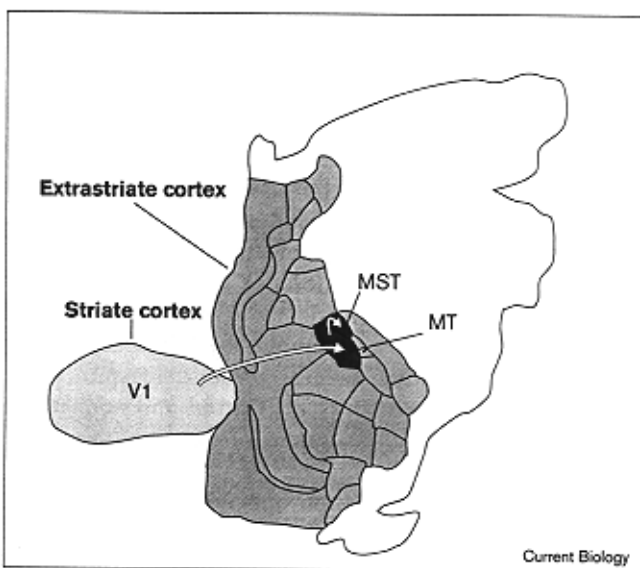
the focus of expansion of radial motion [13], and to the differences between the movement speed in the center and periphery of the full field motion [14].

These neuronal characteristics are, however, only correlational; they show that MST neurons could carry out the computations required for optic flow, not whether they actually do. This is a generic problem in relating single neuron activity to behavior, and it has been solved by either removing the signal generated by the neurons, usually by removing the neurons themselves, and seeing if the particular behavior survives, or by introducing the signal to see if the behavior is modified in a predictable manner, or preferably both. At this point, there is only one published study indicating that monkeys even respond to optic flow — simulated optic flow patterns that activate MST neurons were found to alter monkeys' postural stance [15].

Britten and van Wezel [16] recently addressed this problem by training monkeys to indicate the side of a display that has the focus of optic flow expansion, as in Figure 1a and c, and by showing that these discriminations are changed when the activity of MST neurons is altered by electrical microstimulation. The monkeys were required to indicate on successive displays where the focus of expansion of the optic flow pattern was located along the horizontal meridian of the display, a task that has been used repeatedly in humans. The experimenters then localized MST regions in which neurons along the path of the recording electrode responded to radial expanding patterns — and frequently to other patterns as well — whose foci of expansion were located either to the left or to the right (Figure 1a,c) of the straight ahead position. By passing a small electrical current through the microelectrode at frequencies about equivalent to the highest sustained discharge rate of these MST neurons, they could artificially introduce a signal that should mimic that produced by the neurons.

If MST neurons contribute to the determination of heading, then the neurons activated by electrical stimulation should interact with those neurons that are responding to the simultaneously presented visual stimulus, and the monkey's indication of the heading location should be altered. This is what Britten and van Wezel [16] indeed found at many stimulation sites. The shift was in the direction expected from the combined effect of the activated neuron's preference and the visual stimulus — for example, when the artificially activated neurons were ones with a preference for left heading, the shift in the monkey's discriminations was to the left of where they would be from the visual stimulus alone. These experiments provide the first evidence going beyond a simple correlation that the MST neurons contribute to the computations underlying optic flow, and specifically the determination of heading.

Figure 2



Location and comparative size of MST in the extrastriate cortex of an Old World monkey. Areas of the visual cortex are shaded on the unfolded two-dimensional map of the monkey cerebral cortex. Motion processing in the visual pathway, indicated by direction-selective responses, begins in the striate cortex (V1, blue) which projects to the middle temporal area (MT, green) which in turn projects to the medial superior temporal area (MST, red). The region of MST highlighted in red is the dorsal part, where neurons are frequently responsive to optic flow stimuli. Note the relatively small area of extrastriate cortex that is specifically related to the analysis of optic flow. (Modified from [20].)

But there are some limitations. In only about two-thirds of the tested conditions that showed a significant effect of electrical stimulation did the monkey shift its estimate of heading in the direction expected from the preferences of the neurons at the site of stimulation. While the lack of any significant effect of stimulation at some sites is not surprising given the artificial activation of an arbitrary group of neurons, the significant shift in the opposite direction is more worrisome. One contributing factor must be the apparent lack of a precise mapping of neurons with the same focus of expansion in MST, as compared with the precision of direction of motion mapping in MT, which would result in stimulating a more heterogeneous population of neurons in MST than in MT.

As Britten and van Wezel [16] also point out, the MST neurons activated usually do not have receptive fields that cover the entire optic flow stimulus, and thus they can only be processing part of the available stimulus information. Furthermore, the effects of stimulation are not limited just to the neurons near the end of the stimulating electrode, but rather must extend throughout the network of neurons connected to the activated MST neurons, and it is this network of neurons that determines behavior. The varied effects of the stimulation clearly do not negate

the basic finding that a complex behavior can be altered by a limited physiological intervention.

A more general issue is whether the behavioral test measures the monkey's heading determination, or whether it measures the monkey's ability to discriminate between different patterns of motion, independently of the perception of heading. In the task, the monkey simply indicates the side of the screen that had the focus of expansion, as in the comparable human psychophysics experiments, and it is an inference that this is a judgement of heading direction. Short of actually having the subject move in the environment, however, this is the best approximation we have at present. Despite these limitations, the experiments by Britten and van Wezel [16] do add considerable support for the view that MST contributes to the computations required to determine the direction of heading from optic flow. We thus now know of a specific region of the cerebral cortex that is likely to play an important role in processing optic flow information, and our understanding of this area is sufficient to support neuronal-based models of the underlying mechanisms [17–19].

References

- Gibson JJ: *The Perception of the Visual World*. Boston: Houghton Mifflin; 1950.
- Warren WH, Hannon DJ: Eye movements and optical flow. *J Opt Soc Am A* 1990, 7:160-169.
- Royden CS, Banks MS, Crowell JA: The perception of heading during eye movements. *Nature* 1992, 360:583-585.
- Zeki S: *A Vision of the Brain*. Oxford: Blackwell Scientific Publications; 1993.
- Tanaka K, Hikosaka K, Saito H, Yukie M, Fukada Y, Iwai E: Analysis of local and wide-field movements in the superior temporal visual areas of the macaque monkey. *J Neurosci* 1986, 6:134-144.
- Komatsu H, Wurtz RH: Relation of cortical areas MT and MST to pursuit eye movements. I. Localization and visual properties of neurons. *J Neurophysiol* 1988, 60:580-603.
- Saito H, Yukie M, Tanaka K, Hikosaka K, Fukada Y, Iwai E: Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. *J Neurosci* 1986, 6:145-157.
- Tanaka K, Fukada Y, Saito H: Underlying mechanisms of the response specificity of expansion/contraction and rotation cells in the dorsal part of the medial superior temporal area of the macaque monkey. *J Neurophysiol* 1989, 62:642-656.
- Tanaka K, Saito H: Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. *J Neurophysiol* 1989, 62:626-641.
- Duffy CJ, Wurtz RH: Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. *J Neurophysiol* 1991, 65:1329-1345.
- Lagae L, Maes H, Raiguel S, Xiao D-K, Orban GA: Responses of macaque STS neurons to optic flow components: a comparison of areas MT and MST. *J Neurophysiol* 1994, 71:1597-1626.
- Graziano M, Andersen R, Snowden R: Tuning of MST neurons to spiral motions. *J Neurosci* 1994, 14:54-56.
- Duffy CJ, Wurtz RH: Response of monkey MST neurons to optic flow stimuli with shifted centers of motion. *J Neurosci* 1995, 15:5192-5208.
- Duffy CJ, Wurtz RH: Medial superior temporal neurons respond to speed patterns in optic flow. *J Neurosci* 1997, 17:2639-2651.
- Duffy CJ, Wurtz RH: Optic flow, posture, and the dorsal visual pathway. In *Perception, Memory and Emotion: Frontiers in Neuroscience*. Edited by Ono T, McNaughton BL, Molotchnikoff S, Rolls ET, Nishijo H. Cambridge: Elsevier Science; 1996:63-77.
- Britten KJ, van Wezel RJ: Electrical microstimulation of cortical area MST biases heading perception in monkeys. *Nat Neurosci* 1998, 1:59-63.
- Perrone JA, Stone LS: A model of self motion estimation within primate extrastriate cortex. *Vision Res* 1994, 34:2917-2938.
- Lappe M, Bremmer F, Pökel M, Thiele A, Hoffmann K-P: Optic flow processing in monkey STS: a theoretical and experimental approach. *J Neurosci* 1996, 16:6265-6285.
- Zemel RS, Sejnowski TJ: A model for encoding multiple object motions and self-motion in area MST of primate visual cortex. *J Neurosci* 1988, 18:531-547.
- Knierim JJ, van Essen DC: Visual cortex: cartography, connectivity, and concurrent processing. *Curr Opin Neurobiol* 1992, 2:150-155.