

Cortical processing of visual motion

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1. Introduction

Instability is one of the most salient features of our visual world. Objects move relative to one another and to ourselves in a nearly ceaseless pattern of change. This activity is an extremely rich source of information about the structure of our environment, providing cues that allow us to predict its future state and interact with it effectively. It is not too surprising therefore that motion perception is one of the most behaviorally significant and well-refined of functions performed by our visual system. Of our basic sensory abilities it is also arguably the one for which we now have the best insights into neural underpinnings. Drawing from recent work in a variety of disciplines, my goal in this chapter is to present a coherent portrait of motion processing mechanisms in visual cortex in the context of motion *perception* and visually guided *behavior*. I will begin by discussing the organization of primate visual cortex with special reference to motion processing pathways. In much of the remainder of the chapter, I will focus on a series of well-defined "problems" that are solved by our motion system, illustrating the ways in which a multi-disciplinary approach has contributed to our understanding.

2. Organization of primate visual cortex

One of the most exciting discoveries over the past 25 years, in all areas of sensory research, has been

the multiplicity of cortical sensory areas. In primates, which rely heavily on vision, it is the *visual* cortex that has reached a pinnacle of complexity. Beginning with the pioneering work of Allman and Kaas and of Zeki, the vast wilderness of visual "association" cortex has succumbed to systematic analysis of regional heterogeneity. Well over twenty *extrastriate visual areas* have been identified to date, some of which are shown in Fig. 1A, forming a mosaic organization within the cortical expanse extending forward from the occipital into the temporal and parietal lobes (e.g., Allman et al., 1981; Desimone and Gross, 1979; Desimone and Ungerleider, 1986; Gattass et al., 1985; Maunsell and Van Essen, 1984; Zeki, 1978). Following a long-standing emphasis on modularity and localization of function, the assumption has been that each of these extrastriate visual areas is functionally specialized. The precise nature of such specializations has proved difficult to demonstrate, although, as we shall see, a notable exception exists for those areas involved in motion processing.

3. Parallel processing streams

Another dominant feature in the emerging picture of visual cortical organization is the presence of two functionally specific pathways. (For detailed reviews see Van Essen, 1985; Livingstone and Hubel, 1988). As can be seen in Fig. 1B, these processing streams are expressed in the parallel and hierarchical nature of anatomical connections

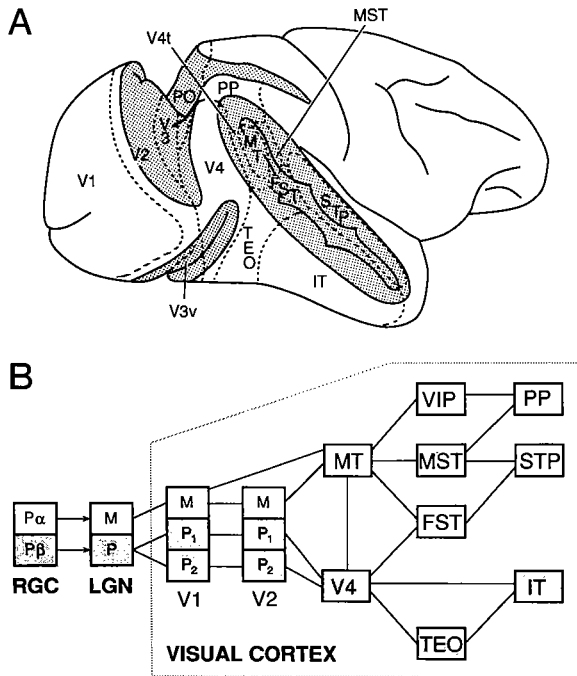


Fig. 1. **A**, Lateral view of the macaque brain showing the location of striate cortex (V1) and some of the extrastriate visual areas. Sulci have been partially opened (shaded regions) to illustrate cortical areas that lie within these sulci. Indicated borders of visual areas (dashed lines) are approximate, particularly anterior to V3. (EC, external calcarine sulcus; IO, inferior occipital sulcus; IP, intraparietal sulcus; LA, lateral sulcus; LU, lunate sulcus; PO, parieto-occipital sulcus; ST, superior temporal sulcus.) **B**, Anatomical connectivity diagram emphasizing hierarchical organization and parallel processing streams along the macaque geniculo-striate-extrastriate pathway. Except where indicated by arrows, these connections have been shown to be both ascending (rightward in this diagram) and descending (leftward), i.e., reciprocal. Not all known components of the magnocellular (unshaded) and parvocellular (shaded) pathways are shown. (RGC, retinal ganglion cell layer; LGN, lateral geniculate nucleus of the thalamus; M, magnocellular subdivisions; P_1 and P_2 , parvocellular subdivisions; see text for additional abbreviations.)

in visual cortex and they transcend visual areas as defined by traditional criteria. The *parvocellular* or *P* pathway is thought to function mainly in form and color vision. By contrast, the *magnocellular* or *M* pathway appears to be largely involved in the processing of visual input pertaining to motion and visual-spatial functions. While this strict functional dichotomy is certainly an over-

simplification and should not be embraced without some reservation, it has heuristic and predictive value and serves to direct our attention to those brain areas potentially involved in motion processing, namely the various components of the *M* pathway.

The *M* pathway originates with the $P\alpha$ retinal ganglion cells, continues through the magnocellular layers of the lateral geniculate nucleus (LGN) and emerges cortically onto layer $4C\alpha$ of area V1. This projects, in turn, to layer 4B. The continuation of this pathway through extrastriate cortex is less discrete and less understood but includes direct (Lund et al., 1975; Ungerleider and Mishkin, 1979) and indirect routes (via areas V2 and V3) to the middle temporal visual area, commonly known as area MT (or V5). Other significant *M* pathway components found at later cortical stages include areas MST (medial superior temporal), FST (fundus superior temporal), PP (posterior parietal), VIP (ventral intraparietal) and STP (superior temporal polysensory).

Functional discrimination of the *M* and *P* pathways comes largely from physiological studies of single neuron response properties. At the level of the LGN, the *M* pathway has been characterized physiologically (relative to the *P* pathway) by fast conduction velocities, transient responses, large receptive fields, a high degree of luminance contrast sensitivity and minimal color selectivity (e.g., Creutzfeldt et al., 1979; Derrington et al., 1984; Derrington and Lennie, 1984; Krueger, 1979; Schiller and Colby, 1983; Schiller and Malpeli, 1978; Wiesel and Hubel, 1966) – properties that seem suited to a role in motion processing. Cortical components of the *M* pathway have been similarly characterized. In addition, the property of directional selectivity emerges to a significant degree as early as layer 4B of V1. Directional selectivity also appears to be a dominant, but not exclusive, feature of the *M* subdivisions of V2 and of V3 and is present in various guises and to varying degrees at later stages in the *M* pathway (MT, MST, FST, PP, VIP, STP) as well.

The undisputed cornerstone of the M pathway is area MT. First described by Allman and Kaas (1971) in the owl monkey and by Dubner and Zeki (1971) in the macaque, area MT is a relatively small (approximately 60 mm² in macaque) visuotopically organized zone (Allman and Kaas, 1971; Zeki, 1974a; Gattass and Gross, 1981; Van Essen et al., 1981) which, in macaques, lies along the posterior extent of the lower bank of the superior temporal sulcus (Fig. 1A). In striking contrast to surrounding cortical areas, some 95% of MT neurons exhibit marked directional selectivity, in combination with a conspicuous absence of selectivity for form or color (Zeki, 1974a; Baker et al., 1981; Maunsell and Van Essen, 1983a; Albright, 1984). It is the salience of these properties that led to the supposition that area MT is a principal component of the neural apparatus for motion processing.

As further affirmation of a significant role in motion processing, MT has been shown to contain a systematic columnar arrangement of directionally selective neurons (Fig. 2) analogous to the orientation column system in V1 (Albright et al., 1984). The scale of this columnar system (≈ 180 deg/500 μ m), in conjunction with the resolution of visuotopic mapping in MT, is such that each point in the visual field is served by a full complement of directionally selective cells (Albright and Desimone, 1987).

In addition to selectivity for direction of motion, some MT neurons – unlike those in V1 – appear to exhibit true speed selectivity, i.e., spatial and temporal selectivities are nonseparable (Newsome et al., 1983). Optimal speed preferences range from 2 to about 256 deg/s with a mode at about 32 deg/s (Maunsell and Van Essen, 1983a; Rodman and Albright, 1987) – a value significantly higher than that found in V1 (Van Essen, 1985). Neurons with similar speed preferences also tend to be clustered in MT.

In general, the sensory response properties of neurons in the more central components of the M pathway (MST, FST, PP, VIP, STP) have not been as well characterized as those in MT. Direc-

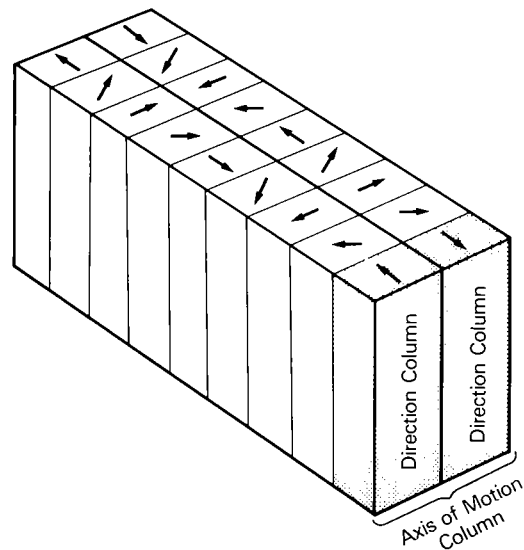


Fig. 2. Three-dimensional idealized depiction of columnar arrangement of directionally selective cells within area MT of macaque. This arrangement is based upon measurements of the rate of change of preferred direction along many electrode penetrations placed at a variety of angles to the cortical surface. The vertical dimension represents cortical depth. The long axis of the figure may be viewed as two complete revolutions of axis-of-motion columns. Moving in this direction one encounters gradual changes in preferred direction. Within each axis-of-motion column (along the short axis of the figure) the two opposite directions of motion along that axis are represented as adjacent columns. (From Albright et al., 1984.)

tional selectivity is a common feature, although there are added complexities and pronounced extra-retinal, particularly oculomotor, influences as well. Some of these will be touched on in the later sections of this chapter.

4. Some problems in visual motion processing

There are a number of central and well-defined problems faced by visual motion processing systems that have been of long-standing interest to perceptual psychologists. Now guided by knowledge of cortical organization, many of these problems are yielding to rigorous neurophysiological investigation in a perceptual context. A few of the best examples follow.

4.1. Establishing spatio-temporal correspondence

Motion perception reduces to the problem of establishing continuity of visual image features in space and time. For ease of illustration we can imagine that we receive the visual world as a series of discrete temporal frames. The problem is that of (1) establishing which parts of each frame correspond to which parts of each preceding frame and (2) detecting the direction of displacement. An important issue concerns the level of image representation upon which this correspondence process operates. There are several possible strategies that a motion detection system might use in order to establish spatio-temporal correspondence. These range from comparisons of "unprocessed" 2-D intensity maps to matches based upon whole object representations. The latter reduces the complexity of the matching problem by taking advantage of real-world constraints (objects tend to exist continuously in space-time), but seems unrealistic since full object recognition does not necessarily precede motion detection. The former has the advantage of simplicity and speed. It has been heavily favored by modelers (Hassenstein and Reichardt, 1956; Van Santen and Sperling, 1985; Adelson and Bergen, 1985; Watson and Ahumada, 1985) and most physiological data from the mammalian visual system are consistent with this type of mechanism (Schiller et al., 1976; Emerson and Gerstein, 1977; Reid et al., 1987).

Luminance-based motion detectors can account for much of what has been referred to as "short-range" (Braddick, 1974) or "first-order" (Cavanagh and Mather, 1989) motion perception. As we shall see, however, such mechanisms fail to account for some important perceptual phenomena, including the simple and telling fact that it is possible to perceive motion of objects that are of luminance equal to their surrounding. An attractive alternative to a strictly luminance-based motion detector is one that operates across a wide range of image segmentation cues, such as texture, color and depth, as well as luminance. Two

recent sets of physiological experiments, in combination with some well-established psychophysics, address the neural bases of such "second-order" (Cavanagh and Mather, 1990) motion processors. The first of these confronts the controversial role of color in motion processing. The second introduces the concept of *form-cue invariance*, which refers to the fact that motion processing is to a large degree insensitive to the cues that define a moving object.

4.1.1. How does color affect motion processing?

The aforementioned system of parallel pathways in visual cortex implies that motion and color are processed independently. Anatomy, physiology, psychophysics and teleology have each contributed to this issue with somewhat equivocal results and it remains a point of controversy (see Livingstone and Hubel, 1987 and Schiller et al., 1990, for example). Much of the debate centers around two main observations: (1) "quality" of perceived motion is sometimes compromised if the moving stimulus is defined solely by color; and (2) cells in the M pathway seem to have limited access to chromatic information.

The perceptual effects are striking and well documented but far from absolute (Dobkins and Albright, 1992). Perhaps the most notable example is the perceived slowing of drifting chromatic gratings relative to luminance gratings (Cavanagh et al., 1983). The magnitude of this effect is, however, sensitive to such variables as degree of chromatic contrast, spatial frequency and location within the visual field. Moreover, few would dispute that motion of a single chromatically-defined object can be perceived.

The physiological data are also suggestive but not conclusive. Although many magnocellular LGN neurons are sensitive to chromatic contrast (Schiller and Colby, 1983), this property is more prevalent in parvocellular LGN (Derrington et al., 1984). Furthermore, cells in layer 4B of V1 exhibit little color selectivity (Livingstone and Hubel, 1984) and the same appears true for the M subdivisions of V2 (DeYoe and Van Essen, 1985;

Shipp and Zeki, 1985) and for V3 (Burkhalter et al., 1986) and MT (Maunsell and Van Essen, 1983a; Albright, 1984), as well. This widely heralded insensitivity to color at various stages of the M pathway would seem to imply the virtual impossibility of true motion perception at chromatic isoluminance – which is clearly not the case. It is important, however, to distinguish color selectivity, *per se*, from the ability of neurons to use chromatic information to detect motion. Given the natural tendency in our visual world for color differences to occur at real object boundaries, one can make a reasonable argument that there is value in a motion system that can rely upon chromatic contrast cues for motion detection – yet the system need not express color selectivity. In support of this view, recent experiments indicate that many MT neurons, while not color selective in the traditional sense, maintain directional selectivity when stimulated with moving stimuli defined solely by chromatic contrast (Charles and Logothetis, 1989; Saito et al., 1989; Dobkins and Albright, 1991). Clearly both psychophysics and physiology indicate that the segregation of motion and color pathways is not absolute. Rather, it may be more appropriate to regard the M and P pathways as recipients of different *kinds* of chromatic inputs as befits their respective contributions to motion and pattern vision.

4.1.2. Form-cue invariant motion processing

Objects in our visual environment are normally distinguishable by a number of cues. In addition to luminance and color these include texture, motion and stereoscopic disparity. Figure-ground segregation is readily accomplished on the basis of any one of these cues alone and objects defined by a single cue can be perceived to move. The percept of motion is, moreover, qualitatively invariant across different cues, a condition unattainable by a strictly luminance-based detector. In an attempt to explain this perceptual invariance, recent physiological experiments have shown that many directionally selective MT neurons exhibit a similar invariance (Albright, 1992; Olavarria et al., 1992). Specifically, for such cells, directional tuning was largely independent of whether the moving stimulus was defined by luminance, texture, or relative motion. About two-thirds of the cells in MT exhibited significant form-cue invariance when tested in this fashion (Albright, 1992). Based upon these results the hierarchical model, shown in Fig. 3, was proposed. According to this scheme, motion detectors in MT operate upon cue-invariant form primitives (e.g., oriented image contours), which are represented at an earlier stage, perhaps V1 or V2, following convergence of information from different cues. The significance of these results lies largely in the fact that motion-sensitive MT neurons are encoding direc-

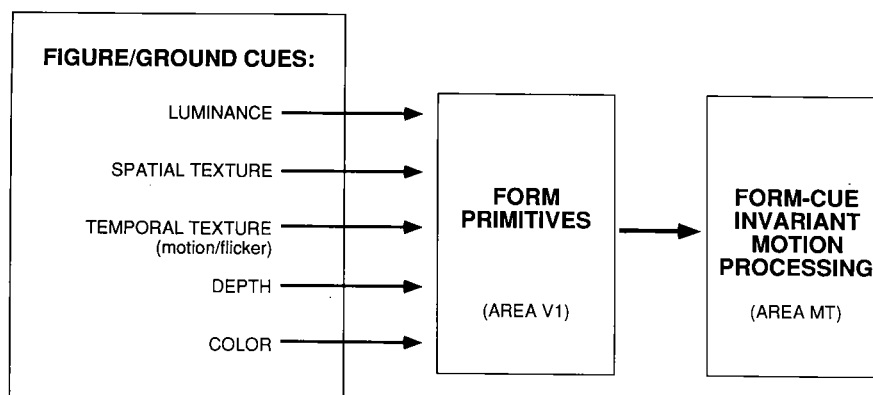


Fig. 3. Proposed system for form-cue invariant motion processing.

tion despite radically different physical stimulus conditions, thereby exhibiting the same sort of qualitative invariance that is manifested perceptually. Information about the defining attributes of image features is sacrificed by this motion system to gain more uniform sensitivity over the broad spectrum of inputs that characterizes our visual world.

4.2. Motion signal integration

Cortical motion processing appears to be a two-stage process. Up to now, I have discussed the initial motion measurements made by our visual system, which are necessarily spatially restricted by the domain of cortical receptive fields. A general problem faced by the motion system is to integrate these local measurements in order to reconstruct the global velocity field. The problem is complicated by the fact that multiple motion signals may arise from either the same or from different moving objects. Successful motion processing is critically dependent upon integrating only those signals common to each moving object. The nature of this integration process has been the subject of intense research in recent years and a fairly coherent story has begun to emerge (see Albright, 1991; Stoner and Albright, 1992c).

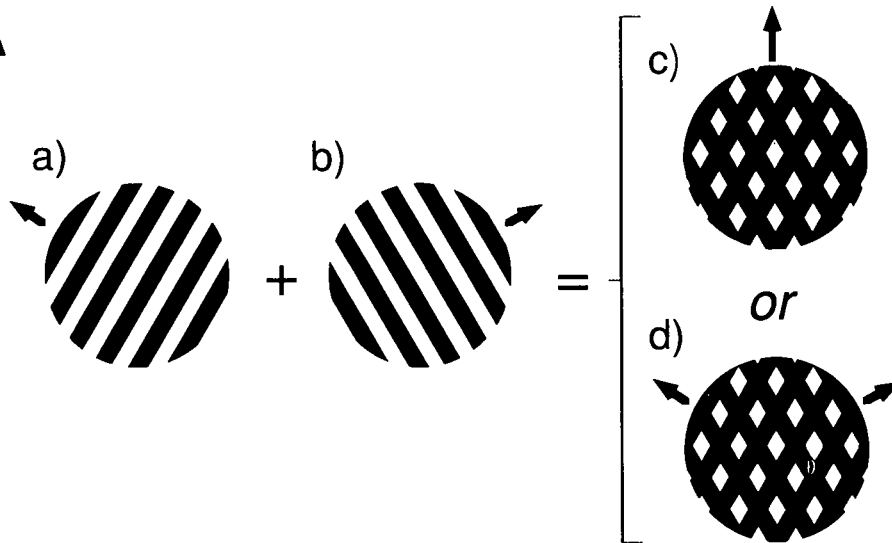
Much of the story centers on the use of "plaid" stimuli developed by Adelson and Movshon (1982). These stimuli afford a conceptually straightforward means to probe the motion integration process both psychophysically and physiologically and have spawned a profusion of experiments (e.g., Gizzi et al., 1983; Movshon et al., 1985; Adelson and Movshon, 1984; Rodman and Albright, 1989; Stoner et al., 1990; Welch, 1989; Ferrera and Wilson, 1987, 1990; Krauskopf and Farell, 1990; Stone et al., 1990; Ramachandran and Rogers-Ramachandran, 1989; Stoner

and Albright, 1992a,b). [Although this plaid paradigm is scarcely the only fruitful approach to motion signal integration (see Nakayama and Silverman, 1983, 1988a,b and Shimojo et al., 1989, for alternative tactics), it has received the widest recognition.] Plaid stimuli, shown in Fig. 4A, are usually produced by superimposition of two sinusoidal gratings. While movement of a single grating is always perceived in a direction perpendicular to its orientation (this is the "aperture problem"), combined movement of the two superimposed gratings generally yields a coherently moving plaid pattern with perceived direction and speed different from either grating alone. Several lines of evidence suggest that local oriented *component motion* (motion of individual gratings) is detected at the first cortical stage. These signals are then integrated by a second cortical stage, providing a representation of true *pattern motion* (motion of the plaid) that is consistent with our perceptual experience.

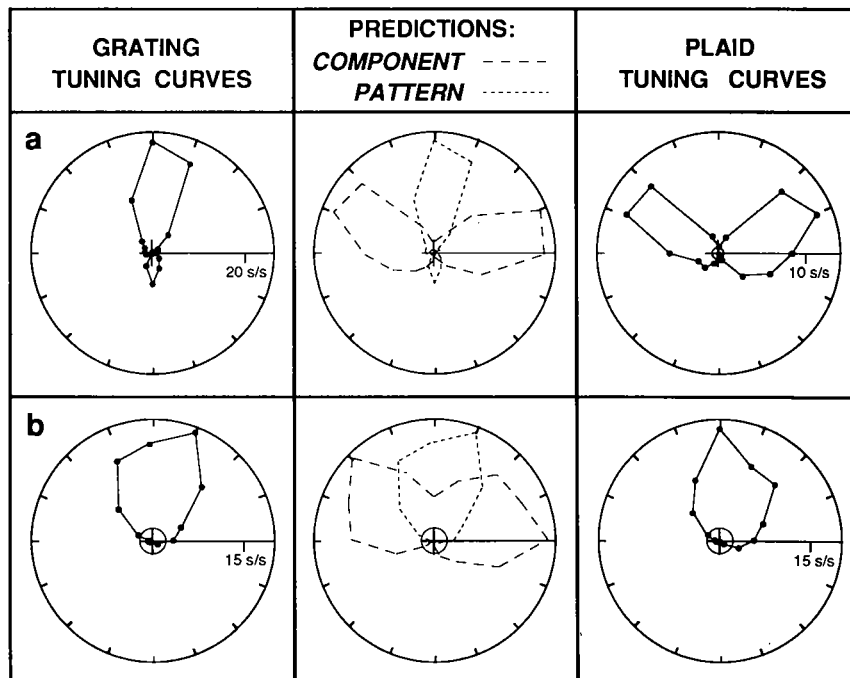
Psychophysical evidence for a two-stage process includes the fact that it is possible to obstruct the integration stage, yielding only a percept of component motion. Adelson and Movshon (1982) found a decline in the frequency of the pattern motion percept when the two gratings differed sufficiently in either spatial frequency or contrast. More recently it has been found that coherence is reduced if gratings are in different stereoscopic depth planes (Adelson and Movshon, 1984), different colors (Krauskopf and Farell, 1990; Kooi et al., 1989), or if one grating is perceived to be transparent and overlaying the other (Stoner et al., 1990). It thus appears that any of a variety of image segmentation cues have the capacity to "gate" the motion integration process. This has the beneficial effect of preventing assimilation of motion signals that arise from different objects so that, for example, we do not combine the motion

Fig. 4. A, Moving "plaid patterns" developed by Adelson and Movshon (1982) are generated by superimposition of two drifting sine-wave gratings. Motions of the component gratings (a and b) are encoded at the first cortical motion processing stage. Under some conditions (see text for details), these component signals are integrated by the second motion processing stage such that perceived direction and speed of resultant plaid pattern (c) differs from that of either grating alone. Under other conditions, only component

A



B



motion is perceived (d). **B**, Data from two MT neurons representing “component” (a row) and “pattern” (b row) stages of motion processing. Direction tuning curves were acquired using a drifting sine-wave grating (first column) or a perceptually coherent plaid pattern (third column). Both cells exhibit a single peak in the grating tuning curve. From these curves, responses to the moving plaid pattern were predicted in accordance with either component or pattern assumptions (second column). The component predictions reflect sensitivity to both oriented components in the plaid pattern. The pattern predictions reflect sensitivity to the composite appearance of the plaid. By definition, the behavior of the component motion neuron conforms to the component prediction while that of the pattern motion neuron conforms to the pattern prediction. (Modified after Rodman and Albright, 1989.)

of shadows with the motion of objects over which they move or the motion of a predator with the motion of adjacent foliage.

These two stages of motion processing are expressed in the properties of cells in the visual cortex. Directionally selective neurons in V1 act as oriented spatial filters (Movshon et al., 1978, 1985; Pollen and Ronner, 1981). This property effectively yields a *neural aperture problem*; a V1 neuron can only detect the component of motion that is perpendicular to its preferred orientation. When stimulated with the plaid patterns, a V1 neuron responds optimally when either of the oriented components is aligned with the orientation selectivity of the cell (Movshon et al., 1980, 1985). True pattern motion is ambiguous from the output of such a cell. The integration process appears to take place in area MT. While many MT neurons (40%), like all V1 neurons, clearly encode component motion, a small population of MT neurons (25%) respond in a way that reflects sensitivity to pattern motion (Movshon et al., 1985; Rodman and Albright, 1989). Examples of the direction tuning obtained from each type of cell are shown in Fig. 4B. In more recent experiments (Stoner and Albright, 1992b) it has been shown that the tendency of an NT neuron to exhibit pattern- or component-type selectivity is correlated with perceptual state; selectivity for component motion is more likely when viewing stimuli that elicit a percept of component motion.

The details of the neural circuitry underlying the transformation from component to pattern motion selectivity are unknown. Several models have been proposed (Adelson and Movshon, 1982; Albright, 1984; Hildreth, 1984; Heeger, 1987; Bülthoff et al., 1989; Albright et al., 1986; Yuille and Grzywacz, 1988; Sereeno, 1989; Sereeno, 1987; Wang et al., 1989). The most appealing and physiologically plausible are those that adopt an "intersection of constraints" solution. In general terms, pattern motion neurons receive converging inputs from an appropriate subset of component motion neurons. Activity of any two

or more component neurons uniquely activates a pattern motion neuron, thereby constraining the solution.

4.3. Motion in three-dimensional space

Up to now, the only type of motion I have considered is translation of rigid objects in the frontal plane. The "primitives" of motion in a three-dimensional world include, in addition to these two axes of translation, motion along the Z-axis (motion-in-depth) and three axes of rotation (Chasles, 1830; cited in Whittaker, 1961). We are exquisitely sensitive to these other classes of motion and have made significant strides toward an understanding of the neural bases of this ability.

There are both monocular and binocular cues for motion in depth. Monocularly, an object moving in depth results in changing retinal image size. Binocularly, motion in depth yields a change in retinal position disparity between the two eyes (Wheatstone, 1838). Zeki (1974b) originally reported the existence of *monocular motion-in-depth neurons* in area MT. These cells are simply selective for changing image size and, at most, appear to constitute a very small fraction of MT neurons (Maunsell and Van Essen, 1983a,b; Albright et al., 1984). A slightly larger population of cells (16%) selectively responsive to changing image size has been found in a restricted region of adjacent area MST (Saito et al., 1986).

Zeki (1974b) also reported *binocular motion-in-depth neurons* in MT, which were characterized by sensitivity to opposite direction preferences in the two eyes (a common manifestation of changing binocular retinal disparity). Although the presence of cells genuinely selective for changing binocular disparity was not confirmed in a subsequent quantitative study (Maunsell and Van Essen, 1983b), neurons responding to changing disparity have been reported to exist in cat areas 17, 18 and lateral suprasylvian cortex (Cy-nader and Regan, 1978; Toyama et al., 1985) and in area V1 of macaque (Poggio and Talbot, 1981).

As Maunsell and Van Essen (1983b) have noted, however, it is essential to rule out the possibility that the appearance of selectivity for motion in depth does not result from the “simpler” conjoint properties of *fixed* disparity selectivity and selectivity for direction of motion in the frontal plane.

Cells sensitive to *rotation* have been found in area MST (Saito et al., 1986; Tanaka and Saito, 1989; Tanaka et al., 1989) but have not been spotted in MT or at any earlier stage in the primate visual system. The rotation-sensitive neurons make up about 14% of the neuronal population in MST and are of two types. Cells of the first type are maximally sensitive to rotation in the frontal plane (“Rf” cells), i.e., about the Z-axis. The second class is maximally sensitive to rotation in depth (“Rd” cells). This group of cells was distinguished by sensitivity to “tilting” in depth of a planar pattern. Although this result is suggestive, we can not infer that these cells encode the velocity gradients associated with rotation of solid objects [as in the “kinetic depth effect” (Walach and O’Connell, 1953)]. Nonetheless, the existence of a rotation-in-depth mechanism within this region of cortex is further supported by the devastating effects of MT/MST lesions on perceived rotation (Siegel and Andersen, 1986; see Section 4.5.2). There are also scattered reports of rotation-sensitive cells (of both types) in posterior parietal cortex (Sakata et al., 1985), STP (Bruce et al., 1981) and frontal cortex (Rizzolatti et al., 1981).

Objects often move along trajectories that can not be characterized as pure linear translation or rotation. Consider, for example, how well we perceive the motion of an autumn leaf as it spirals earthward. The possible paths are infinite in number and it seems highly unlikely that more than a small subset of complex motions are represented in the activity of single cells. Our three axes of translation and rotation, however, form the minimum basis set for representation of any complex motion. This raises the possibility that complex three-dimensional trajectories are represented by a spatio-temporally distributed pattern of activity

among populations of cells sensitive to simple translation and rotation.

4.4. *Detection of motion discontinuities*

Objects rarely move in isolation. A typical visual scene consists of multiple objects at different distances, some of which are moving, some of which are stationary. This relative object motion, made manifest by velocity field discontinuities, is one of the most potent cues available for image segmentation. Any degree of camouflage, which normally confounds luminance, color and texture cues for segmentation, will fail if the hidden object moves. Relative object motion can also be induced by observer self-motion. *Motion parallax* is the term used to refer to the fact that the retinal velocity of images typically varies inversely with distance from their objects to the moving observer (provided that the eyes are not moving to any great extent). As Helmholtz (1924) keenly observed, this systematic relationship between velocity and distance can be utilized to localize objects in three-dimensional space.

A distinct advantage would be afforded to a motion processing system that is capable of using relative motion cues for image segmentation and distance estimation. Allman et al. (1985) have found convincing evidence that such cues are encoded in the activity of a subpopulation of MT neurons. In addition to possessing a discrete excitatory receptive field – the conventional or “classical receptive field” (CRF) – these neurons have large “silent” surround fields. The presence of these surrounds is only detectable from their ability to modulate stimulus-driven activity in the CRF. Broadly speaking, such cells are sensitive to *contrast* between image velocities in the CRF and the surround field. The most common configuration, exemplified by the data shown in Fig. 5, is one in which the cell is selective for maximum directional contrast between center and surround, i.e., the cell responds best when the center is stimulated with its preferred direction and the surround is stimulated by the opposite direction.

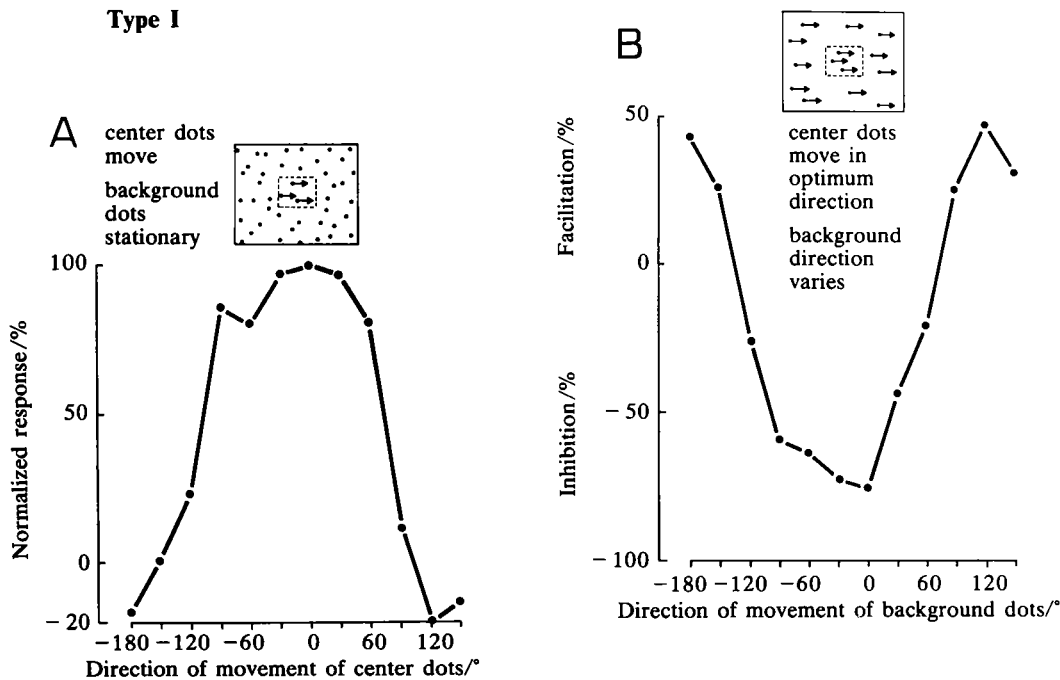


Fig. 5. Modulation of responses of an MT neuron by an antagonistic directionally selective surround. Graph A shows direction tuning for a moving random dot pattern confined to the classical receptive field (CRF). Graph B shows modulation of the response to CRF motion in the preferred direction as a function of the direction of "surround" motion. When center and surround motion were in the same direction (0 deg), the response to CRF motion was suppressed. When center and surround moved in opposite directions (maximum motion contrast), the response to CRF motion was facilitated. (From Allman et al., 1985.)

Not only are these optimal conditions for figure/ground segregation, but this is the state attained from motion parallax when the moving observer's point of fixation lies in a depth plane between the two surfaces. This cell thus seems ideally suited for detecting objects and assigning relative distance. Other cells respond well when a speed difference is present between center and surround, even if direction does not differ. This is, of course, the state attained from motion parallax when both surfaces are in front or behind the moving observer's point of fixation.

The cells studied by Allman et al. (1985) were in area MT of the owl monkey. Similar experiments in the macaque (Saito et al., 1986) indicate that about half of the population of MT neurons in that genus also possess center-surround antagonism. Indeed, this property may be a general

feature of vertebrate motion processing: comparable phenomena have been reported for motion sensitive neurons in cat areas 17 (Orban et al., 1987) and 18 (Orban et al., 1988) and lateral suprasylvian cortex (von Grunau and Frost, 1983) and in the avian optic tectum (Frost and Nakayama, 1983; Frost, 1991, this volume).

The mechanism behind this property remains a mystery. As a general rule, spatial comparisons necessitate long-range connections across cortical maps. These connections may be intra-areal, such as the well-documented lateral connections extending up to several millimeters across area V1 (see LeVay, 1988, for review). Alternatively, they may derive from widely convergent/divergent interareal projections of the type known to exist from V1 to MT (Montero, 1980). The possibility also exists that surround fields develop from

“feedback” projections from higher cortical areas. In any event, the present recognition of center-surround antagonism as one of the most important features of visual information processing will undoubtedly stimulate new studies of its origins.

The presumed relationship between center-surround MT neurons and neural representation of distance has yet to be demonstrated explicitly. Many MT neurons are selective for nonzero stereoscopic disparity (Maunsell and Van Essen, 1983b). One appealing possibility is that MT neurons combine information from stereoscopic disparity and motion parallax cues (stereopsis and “kineopsis”) (Nakayama and Loomis, 1974) – and perhaps from other distance cues such as occlusion, shading and texture gradients – to yield a “cue-invariant” depth map.

4.5. Structure from motion

Relative motion of image features is a powerful cue for the shapes of objects, which is not lost on the primate visual system. It is useful to consider separately two types of relative motion (Ramachandran et al., 1988), the combination of which can be used to infer shape: (1) discontinuities; and (2) gradients in the local velocity field.

4.5.1. Shape from velocity-field discontinuities

Discontinuities in the local velocity field almost always occur at object boundaries (as, for example, when one object passes in front of another) and the envelope formed by these discontinuities aids significantly in object identification. We have already considered physiological evidence for a center-surround receptive field organization that detects motion discontinuities (Section 4.4). Once detected how do they enter into a neural representation of shape? The answer is far from clear. What is clear, from a host of neuropsychological and neurophysiological studies, is that inferior temporal (IT) cortex – the terminus of the P (form processing) pathway – plays a crucial role in shape recognition. Many IT neurons are selective for complex shapes (Gross et al., 1972;

Schwartz et al., 1983; Desimone et al., 1985) and IT lesions cause massive impairments of object recognition (Gross, 1972; Dean, 1982). Although these characteristics of IT cortex were assessed using stimuli defined by brightness discontinuities, it seems likely that motion discontinuities also feed into the encoding of shape by IT neurons (yielding, perhaps, a cue-invariant shape representation). As preliminary support for this possibility, Britten et al. (1991) have found that IT lesions impair the ability of rhesus monkeys to discriminate previously learned shapes defined solely by motion discontinuities. Further work is needed to determine the route through which this motion information enters the form pathway.

4.5.2. Three-dimensional shape from velocity gradients

An even more impressive contribution of motion to form vision is evident from our ability to perceive the three-dimensional shape of a moving object solely from smooth velocity gradients along the object’s surface. The classic demonstration of this phenomenon is the “kinetic depth effect” (Wallach and O’Connell, 1953) in which the velocity field produced by a two-dimensional projection of the points on the surface of a rotating cylinder is sufficient to reconstruct the cylinder’s three-dimensional shape. Although this problem has drawn rapt attention from psychophysicists and modelers, virtually nothing is known of its neural basis. Andersen and colleagues (Siegel and Andersen, 1988; Husain et al., 1989; Treue et al., 1990) have argued from psychophysical data that the mechanism involves a form of three-dimensional surface interpolation from local velocity gradients. One implication is that there may be a stage of motion processing in which cells respond to gradients of velocity within their receptive fields. These hypothetical cells would thus encode slant or curvature of rigid surfaces in three-dimensional space. Such cells have yet to be discovered. Siegel and Andersen (1986) have, however, found that MT/MST lesions impair the ability of rhesus monkeys to

perceive three-dimensional shape from motion. While this result indicates that MT/MST provides motion information that is crucial to the task, it does not imply that MT/MST neurons detect smooth velocity gradients or encode three-dimensional shape.

A much more complex three-dimensional shape-from-motion percept is elicited by what has come to be known as "biological motion", i.e., the highly nonuniform and idiosyncratic velocity gradients characteristic of an animal in locomotion. As Johansson (1975) has so elegantly demonstrated, human observers are remarkably sensitive to biological motion and can identify species, sex and, in some cases, specific individuals in the absence of any other cues. This special case of structure from motion may come about through a mapping of velocity gradients associated with specific body movements or gestures onto specific representations of body shapes. The neural mechanisms involved are entirely unknown. There are, however, anecdotal reports (e.g., Bruce et al., 1981) and one systematic study (Perrett et al., 1985) implicating motion sensitive neurons in the anterior-dorsal regions of the macaque temporal sulcus (area STP). Some of these cells have been shown to respond strongly to specific body or limb movements but failed to respond when the velocity fields were not interpretable as biological motion. These results are a long way from proving the point but they provide the first hint of high-level motion analysis by cortical neurons.

4.6. Optic flow

As an animal moves through the visual world, its vantage point is continually changing. The result is a time-varying alteration of the retinal image, commonly known as *optic flow* (Gibson, 1950). To a first approximation, optic flow patterns consist of radial (centrifugal) streaming of the retinal image with a locus of expansion that often coincides with direction of gaze. A number of studies have shown that optic flow patterns are a rich source of visual "expropriospecific" informa-

tion (Lee, 1980), i.e., information about the position, orientation and movement of one's body relative to the environment (e.g., Gibson, 1950; Koenderink, 1986; Clocksin, 1980; Warren and Hannon, 1988). This information may be used for such tasks as determining direction of self-motion, establishing "time-to-contact" with objects in one's visual field and maintaining balance. In addition to egocentric orienting functions, optic flow aids in image segmentation and establishing the relative locations and shapes of objects in three-dimensional space.

4.6.1. Centrifugal direction biases

Optic flow is thus a common feature of our visual experience that carries substantial information. Much benefit would be afforded to a motion system specially designed to process this information. A salient and often present characteristic of optic flow patterns is motion that is centrifugal with respect to center of gaze. Consistent with this bias, a recent study (Albright, 1989) found an overabundance of directionally selective MT neurons tuned to centrifugal motion. Moreover, in accordance with the fact that direction of optic flow is more variable and speed is typically slower within the "central" portion of the visual field, the centrifugal bias was only found to be present among neurons beyond 12 deg from the center of gaze. A similar centrifugal bias has been observed in cat lateral suprasylvian cortex (Rauschecker et al., 1987), the putative feline homologue of area MT.

Cells preferring motion along paths radiating from the center of gaze have also been reported to exist in area PP of macaque parietal cortex (Motter and Mountcastle, 1981) and in the superior temporal polysensory area (Bruce et al., 1981). These cells differ from those in MT in that they have what Motter and Mountcastle have referred to as "opponent vector organization" of directional selectivity. Typically such cells possess large bilateral receptive fields. Some respond best to motion away from the center of gaze *at any point within the receptive field*, while others respond best to motion toward the center of gaze. Like the

centrifugal MT neurons, these cells appear ideally suited for processing optic flow.

4.6.2. *Depth-dependent motion processing: establishing direction of self-motion from optic flow*

One potentially important use of optic flow is to provide information that can help to establish direction of self-motion, i.e., one's own path of locomotion relative to objects in one's environment. During self-motion, the images of different objects commonly move across the retina with different speeds and directions – varying with object distance in accordance with the motion parallax phenomenon (see Section 4.4). Objects more distant than the point of visual fixation move in the same direction as self-motion, while those nearer move in the opposite direction. It follows that direction of self-motion can be determined from retinal motion if (and only if) direction of each retinal image motion can be linked with distance to the corresponding object. A recent study by Roy and Wurtz (1990) yielded the rather remarkable finding that the optimal direction of motion for many neurons in area MST is dependent upon the retinal disparity – an important cue for relative distance – associated with the moving object. A cell might, for example, prefer rightward image motion when retinal disparity of the moving image reflects a position nearer than the fixation point. The same cell would, however, prefer leftward image motion when disparity reflects a distant position. The depth-dependent motion processing expressed by these conjoint selectivities is precisely what is needed to reconstruct direction of self-motion from retinal image motion.

5. Cortical function and motion perception

The lengthy series of experiments I have described thus far, provide evidence suggesting that activity of MT neurons mediates much of our perceptual experience of motion. These attempts to establish a relationship between cortical func-

tion and visual perception are, however, necessarily correlational and indirect. Our convictions are bolstered by some recent experiments that have managed to address this issue more directly. These fall into three classes: (1) behavioral/perceptual effects of discrete cortical lesions; (2) simultaneous monitoring of neural activity and perceptual choice; and (3) behavioral/perceptual effects of cortical microstimulation.

5.1. *Effects of MT lesions on perceived motion*

If area MT is a crucial component of the neural substrate for motion perception, then we should expect its removal to significantly impair ability to perceive motion. Using small quantities of chemical neurotoxins (such as ibotenic acid) to make discrete lesions of area MT, two laboratories (Newsome and Paré, 1986, 1988; Siegel and Andersen, 1986) have found significant elevation of psychophysical thresholds for motion detection in the absence of impairments of other visual functions. Newsome and Paré used a stochastic motion display in which the “strength” of a motion signal can be varied in the presence of a noisy background. The display, illustrated in Fig. 6A, consists of a dynamic random dot pattern in which some fraction of dots are displaced uniformly in the same direction, while the remaining dots are displaced randomly. If the motion signal strength (% correlated dots) is sufficiently great, motion is perceived in the common direction of the correlated dots; for weaker signals only random flicker is perceived. In these experiments, motion was presented in one of two opposing directions and rhesus monkeys were trained to indicate perceived direction over a range of signal strengths. Direction discrimination thresholds were obtained from the psychometric functions that relate discrimination performance to motion signal strength. Prior to an MT lesion, thresholds were typically as low as 4% (Fig. 6B). Following a unilateral injection of ibotenic acid into MT, however, thresholds were markedly elevated in the hemifield represented by the ablated cortex

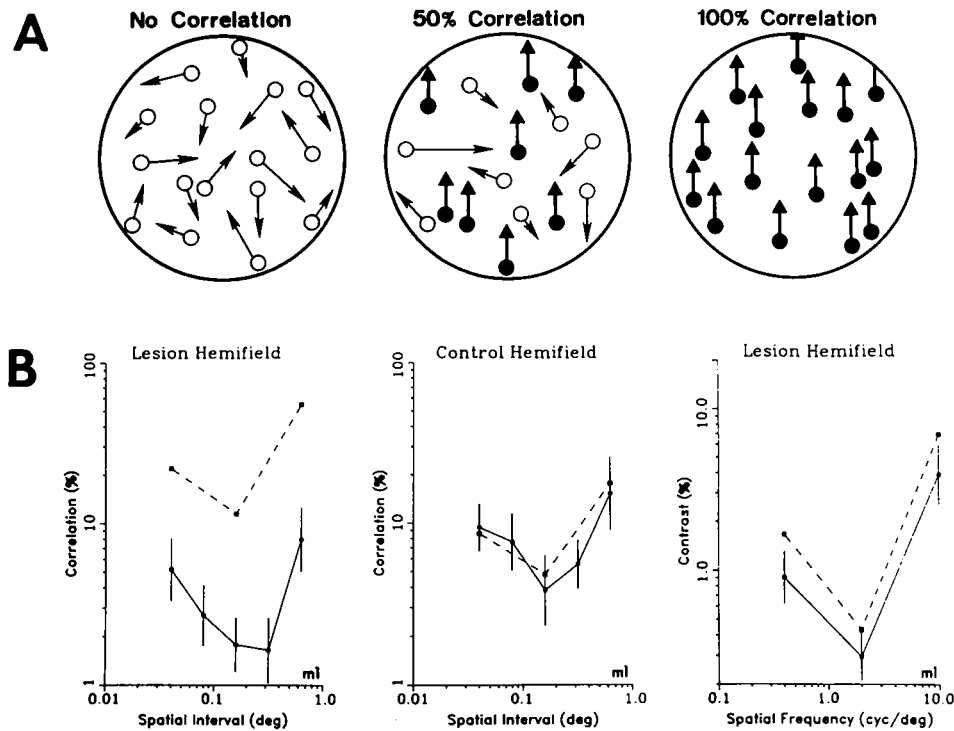


Fig. 6. A, Stimulus employed by Newsome and colleagues to study motion processing in area MT. The display consists of a dynamic random dot pattern in which some fraction of dots ("% correlation") are displaced uniformly in the same direction (indicated by filled dots), while the remaining dots are displaced randomly (unfilled dots). Direction and speed of displacement for each dot are indicated by angle and length of associated vector. (In the actual display all dots are same size and brightness.) Motion signal strength is determined by percent correlation. Examples of weak (left), intermediate (center) and strong (right) signals are shown. Psychophysical threshold for motion discrimination is determined by the minimum signal strength at which direction of motion in this display can be reliably reported. *B*, Effects of a single unilateral MT lesion on motion (using the display shown in *A*) and form processing (spatial contrast detection). Left: motion discrimination thresholds are plotted as a function of spatial displacement interval (i.e., the average distance over which dots are displaced between each temporal frame of the moving display) for data collected before (solid line) and 24 h after (dashed line) the MT lesion was made. Massive postlesion elevation of motion detection threshold is evident. Center: motion thresholds in the control hemifield were unaffected. Right: spatial contrast sensitivity thresholds for sine-wave gratings are plotted as a function of grating spatial frequency. This measure of form perception was unaffected by the MT lesion. (After Newsome and Paré, 1988.)

(Fig. 6B); performance in the control hemifield was unaffected. Contrast sensitivity was also found to be normal in the lesion hemifield (Fig. 6B), ruling out the possibility of a more general visual or motivational deficit.

In a conceptually similar series of experiments Siegel and Andersen (1986) found that MT lesions had devastating effects on the ability of rhesus monkeys to detect two- or three-dimensional structure in moving dot patterns. Contrast sensitivity was unimpaired. The animals studied

by both groups thus appeared to suffer a profound and selective impairment of motion perception following removal of area MT. As is often the case following cortical damage, there was substantial recovery of function with passage of time, suggesting some plasticity of the remaining cortical tissue or development of compensatory strategies. Nonetheless, in combination with previous physiological data, these results provide rather convincing support for the claim that activity of MT neurons contributes to perception of motion.

Selective impairment of motion perception has also been taken as evidence for an MT homologue in human visual cortex. Although human cortical damage is commonly capricious and fails to respect boundaries of functionally specific areas, Zihl et al. (1983) reported a case of a woman with a small bilaterally symmetric lesion near the occipito-temporal junction. Careful testing revealed a massive impairment of motion perception, while acuity, form, color and depth vision remained intact. More recent evaluation of this patient (Baker et al., 1990) using the stochastic motion display (Fig. 6A) employed by Newsome and Paré (1988), revealed a threshold elevation not unlike that seen in rhesus monkeys following MT ablation. These results implicate damage to a human cortical zone that is at least functionally equivalent to area MT. This conclusion has received some validation from other sources. First, studies of metabolic activity levels in human cerebral cortex using positron emission tomography (PET) in conjunction with moving visual stimuli have revealed a locus of activity in approximately the same location as the damage suffered by the Zihl et al. patient (Miezen et al., 1987). Second, in human postmortem tissue a heavily myelinated zone has been identified (Serenó et al., 1988), which appears to correspond spatially to the region distinguished by lesion and PET data.

5.2. Neuronal activity in MT and perceptual choice

Another powerful technique for establishing links between cortical function and perception involves demonstrating temporal correlations between neuronal activity and a behavior that is presumed to reflect perceptual state. This approach has been taken recently in an elegant experiment conducted by Newsome et al. (1989). Activity of single MT neurons was recorded while monkeys were engaged in a psychophysical motion discrimination task. The task was identical to that previously employed by Newsome and Paré

(1988) to study effects of MT lesions (see Fig. 6A). Once an MT neuron was isolated, moving stimuli were presented in either the cell's preferred or null direction at varying motion signal strengths.

If, as we expect, activity in MT plays a significant role in perception of motion, such activity should be correlated with a decision based upon that percept. Indeed, Newsome et al. found that the difference between the magnitude of response in a cell's preferred and null directions was highly correlated with the monkey's ability to discriminate the two directions: at motion signal strengths above the psychophysical threshold the preferred and null responses differed greatly, while below-threshold stimuli usually yielded no difference (Fig. 7A). "Neurometric" functions based on each cell's ability to discriminate direction for motion signals of varying strength compare well to psychometric functions derived from behavioral data obtained simultaneously (Fig. 7B). In other words, the discriminative capacity of an MT neuron covaries with that of the monkey.

Another important paradigm for exploring the relationship between neural activity and perceptual choice is furnished by the phenomenon of perceptual metastability. Under appropriate conditions it is possible to achieve a disassociation between the physical properties of a stimulus and the percept elicited by the stimulus, such that identical stimuli yield different percepts at different times. (A classic and familiar example of perceptual metastability is that elicited by the Necker cube.) Ideally we would like to see a correlation between neuronal activity and perceptual choice under physically invariant but perceptually metastable stimulus conditions.

Logothetis and Schall (1989) adopted this paradigm to further strengthen the case that MT activity mediates perceived motion. They capitalized upon the metastability associated with binocular rivalry. When the two eyes view different images, binocular fusion becomes impossible and perceptual state alternates between the two rivalrous stimuli. Thus, if opposite directions of mo-

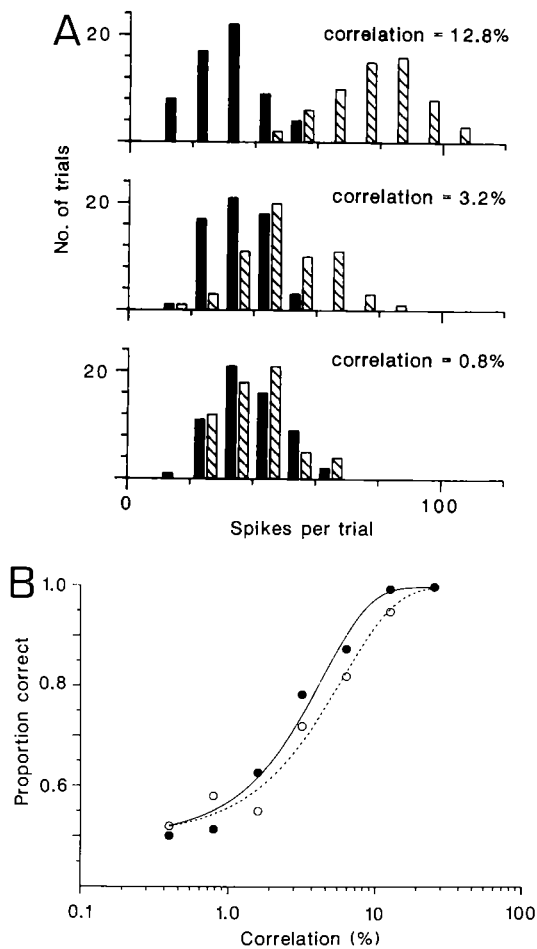


Fig. 7. Comparison of neural activity in area MT with psychophysical performance on motion detection task. The animal was required to detect a motion signal of variable strength in the presence of dynamic random noise (see Fig. 6A). **A**, Responses of a single directionally selective MT neuron at three different motion signal strengths (% correlation). Hatched bars represent preferred direction responses and dark bars represent null direction responses. Preferred and null direction responses are easily differentiable at 12.8% correlation, a signal strength well above psychophysical threshold. Responses are barely separable at 3.2%, a value near psychophysical threshold and indistinguishable at 0.8%, a value well below threshold. **B**, A measure of discriminability of preferred and null responses was computed for a range of correlation levels and used to generate a "neurometric function" (open circles). The neurometric function for this neuron compares well with the standard psychometric function for the direction discrimination task (filled circles). (From Newsome et al., 1989).

tion are presented to the two eyes, both directions will be seen with equal probability but only one direction will be seen at a time. Rivalrous motion stimuli were placed within the receptive field of single MT neurons and rhesus monkeys were asked to report perceived direction. Each cell's preferred direction (assessed under nonrivalrous conditions) was compared to responses obtained when either that preferred or the opposite direction was perceived. About one-quarter of the neurons in their sample responded in a way that reflected perceptual choice. These results, together with those from Newsome et al. provide further compelling evidence that activity of directionally selective MT neurons underlies perceived motion and mediates decisions based upon this percept.

5.3. Effects of MT microstimulation on perceived motion

If, as the aforementioned results imply, activity of directionally selective MT neurons mediates perceptual choice, then it should be possible to influence behavior (and, implicitly, perception) in a predictable fashion by electrically stimulating small groups of cells. Salzman et al. (1990, 1992) obtained precisely this result in rhesus monkeys trained to indicate perceived direction of motion. Using a stochastic motion display identical to that used for the previously described lesion and recording studies (see Fig. 6A), animals viewed repeated trials with motion signals at or near the psychophysical threshold. By exploiting the known clustering of preferred directions in MT (Albright et al., 1984), these investigators were able to electrically stimulate small groups of cells of similar direction preference. Stimulation effected a significant behavioral response bias in favor of the preferred direction at the stimulation site. These results are particularly thrilling because they suggest, perhaps more strongly than any other, a *causal* relationship between neural activity in MT and perceptual choice.

6. Eye movements and cortical motion processing

6.1. Motion as a trigger for smooth pursuit eye movements

The purpose of smooth pursuit eye movements is to stabilize the image of a moving object with respect to the retina. This is accomplished by a neural servo-loop that attempts to match eye velocity with target velocity. Visual inputs to this system must, therefore, carry accurate information about the direction and speed of target motion.

Multiple lines of inquiry implicate areas MT and MST as the major routes through which visual motion signals enter the oculomotor pursuit loop. First of all, there is an abundance of neuroanatomical data demonstrating that MT/MST furnish a large projection to the dorsolateral pons (Glickstein et al., 1980; Ungerleider and Desimone, 1986; Maunsell and Van Essen, 1983c) – a brainstem region known to be involved in the production of smooth pursuit eye movements (Mustari et al., 1988; Suzuki et al., 1990; May et al., 1988). Physiological data linking MT/MST to pursuit generation are also plentiful and diverse. Lisberger and Westbrook (1985) have noted that some of the visual stimulus parameters that influence smooth pursuit, such as speed and direction of motion, also affect responses of single MT neurons. In the same vein, Movshon and Lisberger (1990) have recently found intriguing correlations between the dynamics of pursuit eye movements and temporal characteristics of neuronal responses in MT.

In a comprehensive study of visual and pursuit-related responses in MT and MST, Wurtz and colleagues (Komatsu and Wurtz, 1988a,b; Newsome et al., 1988) found subpopulations of cells possessing properties that seem ideally suited for a role in oculomotor pursuit. These cells, which are most commonly found in the lateral wing of area MST (MSTl), have large receptive fields that include the fovea and are directionally selective

for small spots but exhibit little sensitivity to large-field moving patterns. Many respond during pursuit even when there is no retinal slip of the pursuit target. The latter marks the presence of an extraretinal input relaying information about movement of the eyes, either in the form of a “copy” of the efferent motor command or proprioceptive feedback from the extraocular muscles. The pursuit response of these neurons is always tuned for the same direction as the visual motion response. Sakata et al. (1983) found neurons with similar properties in what appears to have been MST and referred to them as “isodirectional”. Komatsu and Wurtz (1988b) suggest that the visual response is ideal for detecting retinal slip of targets that exceed eye velocity during pursuit. This could provide a retinal error signal for pursuit generation centers to increase eye velocity during pursuit. The extraretinal pursuit response of the same cells may supply a recurrent loop for perpetuating pursuit in the absence of retinal slip (such as, for example, when the object you are pursuing momentarily passes behind a tree) and permits velocity estimation of pursued targets.

Perhaps the most direct evidence for the contribution of motion processing areas MT and MST to smooth pursuit comes from studies of the effects of discrete cortical lesions. If MT and MST do provide information about target velocity needed to initiate appropriate movements of the eyes, then damage to these areas should impair pursuit accuracy. Newsome et al. (1985) employed the neurotoxin ibotenic acid to make small lesions of MT in rhesus monkeys that were trained to make pursuit eye movements to visual targets. Two types of pursuit deficits were observed.

The first deficit concerns the *initiation* of pursuit. Following the onset of target motion it normally takes at least 80 ms for the eyes to begin to move. In order to match eye and target velocity, the oculomotor system must receive an accurate signal reflecting target direction and speed during this initial phase. These first visual motion signals influence performance of the system dur-

ing the immediately ensuing open-loop phase. Pursuit velocity during this period provides a convenient assay for quality of the afferent motion signals. In their experiments, Newsome et al. measured pursuit velocity after ablating a restricted nonfoveal portion of MT in one hemisphere. If target motion began within the portion of the visual field topographically coincident with MT damage, a pronounced reduction of pursuit speed was seen during the first 200 ms after the eyes began to move, i.e., the open-loop phase. Although this resulted in an initial disparity between target and eye position, the situation was corrected by a catch-up saccade and pursuit continued normally once the target emerged from the "motion-blind" zone. This pursuit initiation handicap is presumed to reflect an obstruction of the flow of information from sensory to motor components of the pursuit system.

The second type of deficit pertains to the *maintenance* of pursuit rather than its initiation. This was seen following unilateral lesions of area MT or MST that destroyed cells with foveal receptive fields (Dürsteler et al., 1987). Such lesions yielded a chronic pursuit speed deficit. Thus, while corrective saccades made during pursuit served to refoveate the moving target, visual motion signals arising from the foveal region were chronically compromised by the absence of foveal MT/MST and correct pursuit speed was never attained. Somewhat surprisingly, this chronic pursuit deficit was only seen when pursuit was attempted toward the side of the lesion. The reason for this directional dependence is quite unclear but ipsiversive pursuit deficits are a common symptom of damage to occipital and parietal cortex (e.g., Lynch and McLaren, 1982; Tusa et al., 1986).

A similar directionally specific pursuit aberration has been seen following electrical microstimulation at sites in MT and MST (Komatsu and Wurtz, 1989). In contrast to the effects of ablation, however, stimulation typically induced accelerated pursuit toward the side of stimulation and decelerated pursuit in all other directions. Since the effective spread of current was esti-

mated at 300–450 μ , these effects were regarded as resulting from a transient excitatory disruption of a population of cells with many different direction preferences – a sort of a small reversible lesion but of opposite polarity.

6.2. *Eye movements influence perceived motion*

Degree of retinal displacement is routinely dependent upon a combination of object and self motion, yet perceived object motion follows only the former. This implies that our motion processing apparatus is provided with extraretinal signals about the state of motor control. Oculomotor pursuit is one of the commonest forms of self motion and it generates conditions under which retinal and eye motion must be differentiated. A simple example will help to illustrate the problem: if a target moves rightward while the eyes remain fixed in space, its image is displaced across the retina and rightward motion is perceived. If, however, the eyes pursue the target, there is minimal retinal displacement of the target's image yet rightward target motion is still perceived, implying that the motion signal here is at least partially of extraretinal origin. As a general rule, in order to derive target motion – the motion of which we are consciously aware – its retinal displacement velocity must be summed with eye velocity.

Wurtz and colleagues (Komatsu and Wurtz, 1988a,b; Newsome et al., 1988) found a subpopulation of cells in both dorsal and lateral zones of area MST (MSTd and MSTl) that appear to perform the desired summation of retinal and extraretinal signals. Sakata et al. (1978) reported similar cells in posterior parietal cortex (PP), which receives input from MST. Unlike the "isodirectional" MST cells that are implicated in the generation of pursuit (see Section 6.1), these cells boast two types of visual motion selectivities: they respond well to motion of both large-field patterns and small spots but the direction preferences for the two stimulus types are opposed. They also respond during pursuit in the absence

of retinal slip. Pursuit directionality is opposed to the large-field visual response but aligned with the small target response. This constellation of selectivities yields the same response to either pursuit or target retinal displacement *in the same direction*. Both are conditions that could ensue from a single direction of target motion and both yield the same motion percept. The “antidirectional” large-field response of these cells serves to facilitate responses while pursuing a target that is moving in front of a stationary textured background – a common occurrence in the real world. Interestingly, another consequence of the opposition of large and small target directionality is similar selectivity for: (1) a moving target; and (2) a stationary target on a (oppositely) moving background. This indiscriminate behavior may underlie a perceptual anomaly well-known as “induced motion” (Duncker, 1929), in which a stationary target is seen to move in the opposite direction from a moving background. The output of this group of MST and posterior parietal neurons thus combines retinal and oculomotor extraretinal signals of varied nature in a fashion that mirrors perceived motion.

7. Other components of the cortical motion pathway

In this review, I have focused mainly on the roles of areas MT, MST and PP in motion processing, since these are the areas we know most about. Later stages along the M pathway include areas FST, VIP and large expanses of unmapped motion-sensitive cortex that lie in the anterior-dorsal extent of the superior temporal sulcus. From a single study (Desimone and Ungerleider, 1986) we know that FST neurons have very large, often bilateral receptive fields and only one-third are directionally selective in the conventional sense. Some cells only respond to “twisting or rotating complex three-dimensional objects within the receptive field”. Similar anecdotes characterize cells in more anterior parts of the superior temporal sulcus (STP) (e.g., Bruce et al., 1981; Jeeves et

al., 1983) and the possibility exists that these cortical hinterlands harbor cells that encode stereotypic motions of biologically significant images, such as dynamic facial expressions or looming body parts.

Area VIP is a small region that lies along the ventral-anterior portion of the intraparietal sulcus (Fig. 1). It was originally defined neuroanatomically as a recipient of MT projections (Maunsell and Van Essen, 1983c; Ungerleider and Desimone, 1986) and has only recently become a target of neurophysiological investigation. Preliminary reports (Colby et al., 1989; Duhamel et al., 1989) demonstrate large receptive fields and directional selectivity for large moving patterns – properties not unlike those seen in MST. Quite unlike MST, however, many VIP cells possess somatosensory receptive fields that appear to be spatiotopically correspondent with their visual receptive fields. A reasonable (albeit vague) inference from these data is that VIP plays some role in linking the visual and tactile qualities of a proximal moving stimulus. We might even entertain the idea that this linking is designed to occur between visual stimuli of external origin, such as dynamic facial gestures of conspecifics and tactile stimuli of self-origin, such as proprioceptive feedback from our own facial movements. Indeed, a convergent input of this nature would seem ideal for aspects of facial mimicry and empathic interpretation of facial expression.

8. Concluding remarks

“I never saw a sunset like that, Mr Turner,” said the lady. “Don’t you wish you could, madam?”, replied Turner.

The last 10 years have seen unprecedented progress toward an understanding of the cortical mechanisms underlying motion perception. Highlights include the neurophysiologist’s final acknowledgement that the visual life of the mind differs vastly from the sensory array and is in many ways a far richer construct. What we actual-

ly *see* is not simply quilted together piecemeal from a spatially distributed set of feature detectors but, rather, is heavily dependent upon spatial and temporal context, what we have previously seen and known to be, what we expect to see, what happens to be important to us at the time and a myriad of other “cognitive” factors long thought to lie beyond the reach of one’s microelectrode.

Among the foremost of problems now deserving attention is that of image segmentation and reconstruction of the wholeness and object-based quality of perception – the so-called “binding problem” (Köhler, 1967; Sejnowski et al., 1988). This is an exciting and challenging directive but it stresses the flaw in our persistent attempts to study the operation of functional sub-systems, such as that for the analysis of motion, in isolation. Recent interest in the role of temporal interactions among neurons as a means of “binding” together the features they independently encode (Gray et al., 1989; Crick and Koch, 1990) emphasizes an attractive, albeit provocative, approach to this problem. New technological developments, such as optical and multichannel neuronal recording, will afford the opportunity to evaluate temporal interactions among large groups of cortical neurons in behaving, *perceiving* animals.

Clearly, future studies of motion processing (and vision generally) must also place increasing emphasis upon extraretinal factors, particularly attention and memory. Recent neurophysiological experiments by Desimone and colleagues (Moran and Desimone, 1985; Spitzer et al., 1988) and by Maunsell and colleagues (Hochstein and Maunsell, 1985; Haenny et al., 1986; Maunsell et al., 1989) have demonstrated some of the ways in which these factors influence cortical processing of form. Comparable manipulations have not been attempted for the motion pathway. Yet an important new psychophysical finding by Chaudhuri (1990) – attentional gating of the motion aftereffect – suggests that spatially directed attention can have a strong impact on the way we see things move and must, therefore, prejudice motion processing at an early stage in the cortical

hierarchy. Attempts to investigate these extraretinal influences and cooperative neural interactions pose formidable technical challenges but will soon bring us far closer to an understanding of how we see motion and use it to guide our behavior.

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