Structure and Function of Visual Area MT

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Abstract

The small visual area known as MT or V5 has played a major role in our understanding of the primate cerebral cortex. This area has been historically important in the concept of cortical processing streams and the idea that different visual areas constitute highly specialized representations of visual information. MT has also proven to be a fertile culture dish—full of direction- and disparity-selective neurons—exploited by many labs to study the neural circuits underlying computations of motion and depth and to examine the relationship between neural activity and perception. Here we attempt a synthetic overview of the rich literature on MT with the goal of answering the question, What does MT do?

Contents

INTRODUCTION

The middle temporal visual area (MT or V5) of the macaque monkey possesses a number of attributes that have made it particularly attractive to systems neuroscientists. This region is typical of extrastriate cortex but is still readily identifiable both anatomically and functionally. Though extrastriate, it is still quite close to the retina—its principle inputs as few as five synapses from the photoreceptors—a feature which means, among other things, that the mechanisms by which its receptive field properties arise can be profitably studied. And, although MT neurons are near enough to the inputs to be mechanistically tractable, they are also close enough to some outputs—in particular, those involved in eye movements—to provide an easily measurable, continuous readout of computations performed in this pathway. Finally, MT neurons are concerned with visual motion, which is of obvious ethological importance, which has been extensively characterized psychophysically, and for which there are well-defined mathematical descriptions. Much of the work on MT has focused on its role in visual motion processing, though, as we hope to make clear in what follows, MT plays a richer and more varied role in vision.

MT WAS A KEY PART OF THE EARLY EXPLORATION OF EXTRASTRIATE CORTEX

Part of MT's significance is historical; it played an important role in the discovery of new extrastriate visual areas (Felleman & Van Essen 1991) and in the idea that they constitute specialized representations of the visual world (Zeki 1978, Barlow 1986).

At the beginning of the twentieth century, primate visual cortex was thought to consist of only three architectonically distinct fields (Brodmann 1909). Beginning in the late 1940s, however, it became clear that considerably more of the cortex was involved in vision. The first demonstration came from temporal lobe lesions that produced visual impairment (Mishkin 1954, Mishkin & Pribram 1954) unaccompanied by deficits in other sensory modalities (Weiskrantz & Mishkin 1958, Brown 1963). Mapping studies using surface electrodes also revealed visually responsive regions well anterior to those traditionally associated with vision (Talbot & Marshall 1941, Clare & Bishop 1954, Woolsey et al. 1955). In addition, new anatomical techniques (Nauta & Gygax 1954) permitted the labeling of connections after lesions of striate cortex (Kuypers et al. 1965, Cragg & Ainsworth 1969, Zeki 1969), which revealed a direct striate (V1) projection zone situated on the posterior bank of the superior temporal sulcus (STS).

MT was discovered at roughly the same time by two different groups. In England, Dubner & Zeki (1971) were able to record
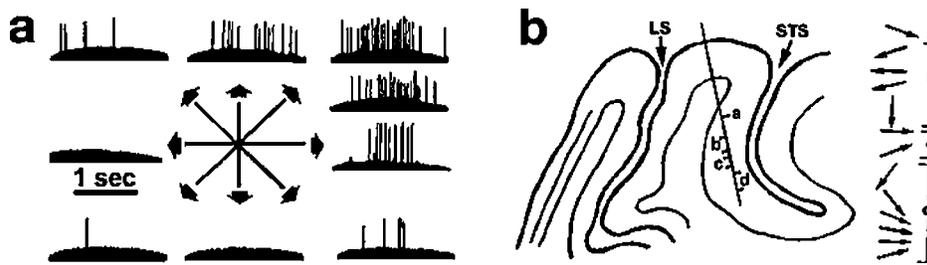
Figure 1

First demonstration of direction selectivity in macaque MT/V5 by Dubner & Zeki (1971). (*a*) Neuronal responses to a bar of light swept across the receptive field in different directions (modified from figure 1 of Dubner & Zeki 1971). Each trace shows the spiking activity of the neuron as the bar was swept in the direction indicated by the arrow. The neuron's preferred direction was up and to the right. (*b*) Oblique penetration through MT (modified from **Figure 3** of Dubner & Zeki 1971) showing the shifts in preferred direction indicative of the direction columns subsequently demonstrated by Albright et al. (1984). See also **Figure 4**.

visual responses from the V1-projection zone in anesthetized macaques, in so doing establishing a number of physiological hallmarks, particularly their direction-selective responses (**Figure 1*a***). Quite presciently, they also suggested a columnar organization for direction-selective neurons (**Figure 1*b***) and a role for MT signals in guiding pursuit eye movements, both subsequently confirmed (Albright et al. 1984, Lisberger et al. 1987). Around the same time, Allman & Kaas (1971) were recording from owl monkeys and using a different approach. They made systematic rows of microelectrode penetrations across the entire cortex, mapping receptive fields as they went, thus discovering a large number of retinotopically organized maps. One of these, which they named MT for middle temporal, mapped onto a well-defined region of dense myelination in the lower layers and contained neurons that responded better to drifting bars than to flashed spots. The myelination was also later shown to be characteristic of the macaque motion area (Van Essen et al. 1981), which Zeki subsequently named V5. This histochemical feature has been an underappreciated factor in contributing to the detail with which MT has been studied because it has permitted reliable comparisons across different studies.

Following the first studies, a series of papers confirmed that MT contained a high concentration of direction-selective neurons in several species of both New and Old World monkeys (Zeki 1974, 1980; Baker et al. 1981; Van Essen et al. 1981; Maunsell & Van Essen 1983a,b; Felleman & Kaas 1984). These studies indicated that MT was both unique as a cortical area highly specialized for visual motion and, at the same time, common to a number of different primate species.

CONNECTIONS

Like every other cortical area, MT has a rich set of interconnections with other regions of the cortex as well as with numerous subcortical structures. These connections have been discussed in previous publications (Felleman & Van Essen 1991, Orban 1997, Lewis & Van Essen 2000), so we do not recapitulate them here. From a broad perspective, MT's corticocortical connections identify it as one of the main inputs into the dorsal or posterior parietal processing stream (Ungerleider & Mishkin 1982, Maunsell & Newsome 1987), and its key outputs target structures that are implicated in the analysis of optic flow (e.g., MST, VIP) and the generation of eye movements (e.g., LIP, FEF, SC, dorsolateral

preferred direction: the direction of motion eliciting the greatest response from a given neuron
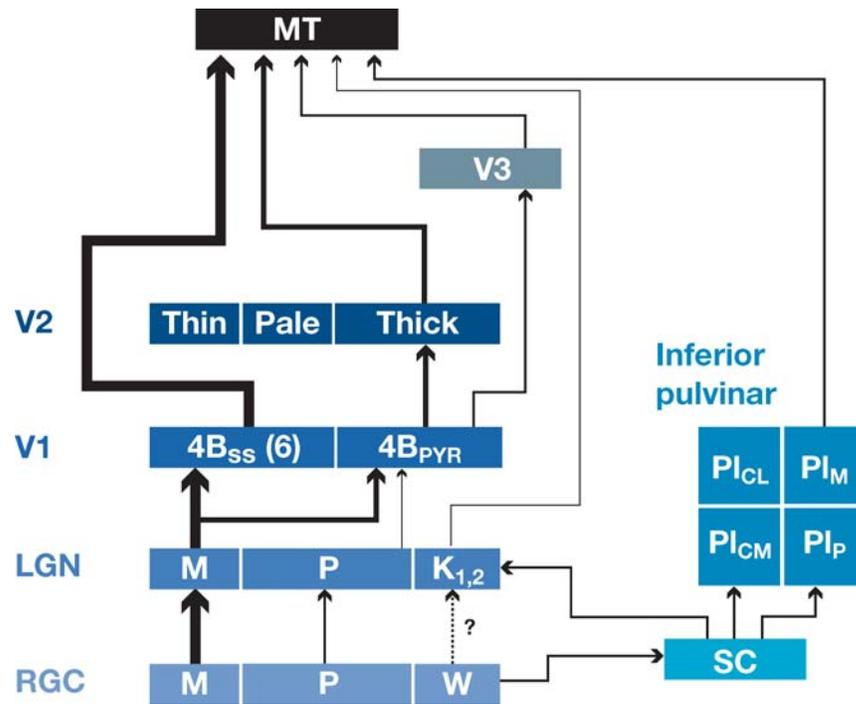
Figure 2

Gestalt map of major routes into MT in the manner of Felleman & Van Essen (1991). Line thickness is roughly proportional to the magnitude of the inputs, on the basis of a combination of projection neuron numbers and, where data are available, the characteristics of their axon terminals (see **Figure 3**). The thickest lines represent the direct cortical pathway emphasized in the text. Following are important caveats: The pathways shown are those discussed in the text and omit a number of known feedforward cortical inputs that appear lesser in magnitude (V3A, VP, PIP) as well as many subcortical inputs. The sources of the direct and indirect projections from V1 are probably not defined purely by cell morphology (i.e., spiny stellate versus pyramidal; see Elston & Rosa 1997), though they are largely distinct; the largest 4B cells contribute to the direct pathway (Sincich & Horton 2003). The precise nature of the retinal inputs to K1,2 is not known, though their response properties are W-like in the galago (Irvin et al. 1986). Also, the proposed input to MT from the SC via the pulvinar is rendered problematic by the finding that, in owl monkey pulvinar, the principle target of SC terminals (PI$_{CM}$) is different from the main source of MT projections (PI$_M$) (see Stepniewska et al. 1999). Abbreviations: 4B$_{SS}$, spiny stellate neurons in layer 4B; 4B$_{PYR}$, pyramidal neurons in layer 4B; LGN, lateral geniculate nucleus; M, magnocellular stream; P, parvocellular stream; K, koniocellular layers of LGN; PI$_{CL}$, central lateral nucleus of the inferior pulvinar; PI$_{CM}$, central medial nucleus of the inferior pulvinar; PI$_M$, medial nucleus of the inferior pulvinar; PI$_P$, posterior nucleus of the inferior pulvinar; RGC, retinal ganglion cells; SC, superior colliculus; VP, ventral posterior area.

pons). Because we desire to address how MT neurons acquire their unique visual response properties and discuss the role they play in motion computations, we focus the present discussion on MT's major inputs (**Figure 2**) and their functional implications. In particular, we argue that the most important input to MT is from a magnocellular-dominated projection originating from layer 4B of V1.

To a first approximation, MT is dominated by cortical rather than subcortical inputs. Nevertheless, unlike some other extrastriate areas such as V2 (Schiller & Malpeli

1977, Girard & Bullier 1989) and V4 (Girard et al. 1991), which are completely dependent on input from striate cortex, at least some MT neurons remain both visually responsive and even direction-selective following removal or inactivation of V1 (Rodman et al. 1989, Girard et al. 1992). In some cases, residual MT function may have been conferred by callosal connections from the intact hemisphere (Girard et al. 1992) and, in other cases, via the superior colliculus (SC) (Rodman et al. 1990). However, although SC lesions completely eliminated residual MT responses after V1 lesions, alone they produced no significant changes in MT responses (Rodman et al. 1990).

Also of interest in this regard is a small, direct LGN input to MT, mainly from koniocellular neurons (Stepniewska et al. 1999, Sincich et al. 2004). Although such a projection could, in theory, explain remaining function in MT after V1 lesions, it is unclear how these LGN cells would convey direction selectivity to MT or why SC lesions would abolish it. Rodman et al. (1990) raised the possibility that extrastriate-projecting LGN neurons did not receive a direct retinal input—supported by the anatomical study by Benevento & Yoshida (1981) in which intraocular injections of tritiated amino acids failed to produce labeling in extrastriate cortex—but instead were dependent on SC inputs for their visual responsiveness. This idea remains an interesting possibility, which awaits a direct test.

Cortical feedforward inputs to MT come from several areas, including V1, V2, V3, V3A, VP, and PIP (Maunsell & Van Essen 1983c, Felleman & Van Essen 1991); those from V2, V1, and V3 are the largest inputs, judging from the numbers of labeled neurons in each area after MT injections (Maunsell & Van Essen 1983c). However, single axon data suggest that the most potent input is probably from V1. These studies show that some V1 inputs to MT are highly specialized (**Figure 3**): They have larger axons (up to 3 μm in diameter, versus 1 μm for other

corticocortical axons; Rockland 1989, 1995) and terminal boutons that are both larger and more complex than those from V2, often forming multiple synapses on a single MT neuron (Rockland 1989, 1995, Anderson et al. 1998, Anderson & Martin 2002). These specializations, which appear unique to the V1-to-MT projection, should combine to provide fast and secure synaptic transmission, though this idea has not received a direct test.

Of the inputs directly from V1, those from layer 4B predominate, at least numerically. After injections of retrograde tracers into macaque MT, more than 90% of the labeled V1 neurons are found in layer 4B; the remaining are found in the large cells of Meynert near the boundary of layers 5 and 6 (Tigges et al. 1981, Maunsell & Van Essen 1983c, Shipp & Zeki 1989a) (**Figure 3a**). These MT-projecting 4B neurons are predominantly spiny stellate in morphology (Shipp & Zeki 1989a) (though, see also Elston & Rosa 1997), are the largest cells in this layer (Sincich & Horton 2003), and appear to receive exclusively M-inputs via layer 4Cα (Yabuta et al. 2001). In addition to this direct V1-MT connection, there are important indirect cortical inputs via V3 (Maunsell & Van Essen 1983c) and the thick cytochrome oxidase stripes of V2 (DeYoe & Van Essen 1985; Shipp & Zeki 1985, 1989b) (**Figure 3a**). These indirect inputs also originate in V1 but from a mostly separate population of neurons within layer 4B (Sincich & Horton 2003) that receives a mixed M and P input (though still predominantly M by a margin of about 2.5:1) (Yabuta et al. 2001) and is preferentially distributed beneath interblob regions (Sincich & Horton 2002). Overall, this anatomical picture is consistent with functional studies, showing that reversible inactivation of the M-layers of the LGN nearly completely abolishes the visual responsiveness of MT neurons, whereas P-layer inactivation has a much smaller, though measurable, effect (Maunsell et al. 1990), the latter presumably mediated by the indirect pathway.

FUNCTIONAL ORGANIZATION

MT is retinotopically organized, each hemisphere containing a more-or-less complete map of the contralateral visual hemi-field, with a marked emphasis on the fovea the central [15° of the visual field occupies over half of MT's surface area (Van Essen et al. 1981)] and a bias toward the lower quadrant of the visual field (Maunsell & Van Essen 1987). Within this relatively crude retinotopic map,

there exist, at finer spatial scales, several other organizations concerning neural tuning for different stimulus parameters.

MT was the first extrastriate visual area for which clear-cut evidence of a columnar organization was discovered. The possibility of direction columns was raised in the initial publication of Dubner & Zeki (1971) but was not shown definitively until more than 10 years later (Albright et al. 1984). Evidence for a columnar organization consisted of relatively smooth changes in the preferred directions of neurons during oblique penetrations through MT, with direction sequences interrupted occasionally by sudden jumps and, in particular, by jumps of 180° more often than would be predicted by chance. To account for their observations, Albright and coworkers proposed a model in which columns of smoothly varying preferred directions ran side by side with a corresponding set of columns preferring the locally opposite direction. This was subsequently supported by functional labeling studies using 2-deoxyglucose (Geesaman et al. 1997). DeAngelis & Newsome later showed a strong columnar organization in terms of tuning for binocular disparity (DeAngelis & Newsome 1999) coexisting with the direction columns (**Figure 4**). There is also a clustering of neurons by speed preference, but the organization is not strictly columnar (Liu & Newsome 2003b).

In the macaque, neurons whose receptive fields possess antagonistic surrounds are more common in supragranular layers, whereas those lacking such surrounds are found predominantly in the input layers (Lagae et al. 1989, Raiguel et al. 1995). In the owl monkey, where direction columns are not well defined (Malonek et al. 1994) and tuning for binocular disparity is rare (Felleman & Kaas 1984, Born 2000), a robust columnar organization exists with respect to center-surround interactions: groups of neurons having antagonistic surrounds interdigitated with neurons that lack such surrounds and therefore respond optimally to wide-field motion (Born & Tootell 1992, Berezovskii & Born 2000, Born 2000). The evidence for such an organization in the macaque is more equivocal: Some investigators have found no consistent organization (DeAngelis & Newsome 1999), and others report a tangential clustering (i.e., parallel to the cortical surface) (Raiguel et al. 1995) in addition to the laminar segregation noted

Figure 4

Functional organization of macaque MT (from DeAngelis & Newsome 1999). Superimposed on the model of direction columns originally proposed by Albright et al. (1984) are the columnar zones of strong (*rainbows*) and weak (*blue*) binocular disparity tuning. Within the zones of strong disparity tuning, the preferred disparities vary in a smooth manner, similar to the direction columns and to orientation columns in V1.

Figure 3

Comparison of two of the major cortical inputs to MT. (*a*) Labeled neurons in V1 (17) and V2 (18) after a large injection of HRP into MT of a squirrel monkey (from figure 8 of Tigges et al. 1981; 40 × magnification). The far greater number of labeled V1 cells in layer 4B (*arrowheads*) as compared with layer 6 (*arrow*) has also been found in the macaque monkey (Maunsell & Van Essen 1983c, Shipp & Zeki 1989a). Note the two well-defined clusters in the upper layers of V2 (*open arrows*), subsequently shown to be confined to the thick cytochrome oxidase stripes (DeYoe & Van Essen 1985, Shipp & Zeki 1985). (*b–e*) High resolution tracers (BDA) demonstrate differences in size and shape of terminal arbors and boutons from V1 (*b, c*) and V2 (*d, e*) within macaque MT (K. Rockland, unpublished data). (*b, c*) Example of a large-caliber V1 axon, with large boutons. Note, however, the mix of large and small boutons. (*d, e*) Field of terminations from V2. Note more uniformly small boutons. The scale bar is 100 μm panels *b* and *d*, and 10 μm in panels *c* and *e*. See also Rockland (2002).

binocular disparity:
a difference in the relative position of a stimulus on each of the two retinas. This disparity is the basis of stereoscopic depth perception.

above. This clustering may occur predominantly in the upper (output) layers of macaque MT because a segregation of center-surround properties appears to exist in subdivisions of one of MT's main projection zones, MSTd versus MSTl (Tanaka et al. 1986, Komatsu & Wurtz 1988, Eifuku & Wurtz 1998). The finding that microstimulation in macaque MT has qualitatively different effects on smooth pursuit eye movements depending on the nature of center-surround interactions at the stimulation site (Born et al. 2000) is consistent with the idea of segregation and, to date, is the only direct experimental evidence to support a role for MT center-surround interactions in the type of figure-ground comparisons originally suggested by Allman and his colleagues (Allman et al. 1985b).

BASIC TUNING PROPERTIES

The visual responses of MT neurons are determined principally by five properties of the stimulus: (*a*) retinal position (*b*) direction of motion, (*c*) speed of motion, (*d*) binocular disparity, and (*e*) stimulus size (due to surround suppression). In the following paragraphs we expand on selected aspects of the above description. The basic visual-response properties of MT neurons have been addressed extensively in excellent reviews by Orban (1997) and Britten (2003), so we focus on more recent studies and on those most relevant to the subsequent discussion. In particular, we attempt, where possible, to compare MT properties with those of its principle inputs, with an eye toward understanding what MT contributes to cortical motion processing.

The principal V1 inputs to MT described above are themselves strongly direction selective (Movshon & Newsome 1996) and also are tuned for speed (Orban et al. 1986). Moreover, given that the most direction-selective V1 cells also tend to be highly selective for binocular disparity (Prince et al. 2000), many of MT's V1 inputs are also likely disparity tuned. Conceivably then, MT neurons inherit three of their most important properties from V1.

So what, then, does MT add? It is chastening to note up front that more than 30 years of physiology have not yielded a clear-cut answer to this question. In a number of cases, early evidence pointed to differences that were theoretically attractive but that, upon closer and more quantitative analysis, failed to materialize. Because these examples are informative, we first consider several of them, before moving on to other differences that have been borne out.

MT receptive fields are much larger than those in V1—a ballpark figure is tenfold greater in linear dimensions—so one might suppose that MT neurons can compute motion and disparity over larger spatial ranges than can V1 cells. This idea was particularly attractive for directional interactions because studies of human perception have revealed at least two different motion-sensing mechanisms that operate over different spatial scales and also differ with respect to other properties, such as contrast invariance (Nakayama 1985). As a result, investigators proposed that MT neurons might inherit short-range motion sensitivity from their V1 inputs but would, in addition, compute motion over longer spatial displacements, commensurate with the size of their receptive fields. Indeed, initial experiments by Mikami and colleagues (1986), using sequences of flashed bars, suggested that MT neurons did produce directional signals to larger spatial separations, on average, than did V1 cells. However, a recent reexamination of this issue, using more directly comparable stimuli revealed very similar upper limits for V1 and MT (Churchland et al. 2004). In fact, the directional interactions of neurons from both areas take place over extremely small spatial ranges—fractions of a degree in receptive fields that are, in MT, many degrees wide (**Figure 5***d–f*)—and they reverse direction for contrast-inverting sequences (Livingstone et al. 2001, Livingstone & Conway 2003), both of which are characteristics of the short-range perceptual

process (Braddick 1974, Anstis & Rogers 1975). Finally, when short-range ($\Delta x \approx 0.13°$, $\Delta t \approx 17$ ms) and long-range ($\Delta x \approx 1°$, $\Delta t \approx 125$ ms) apparent motion cues were pitted against each other in opposing directions, the direction of the short-range motion dominated the responses of MT neurons (Shadlen et al. 1993), whereas the long-range direction clearly dominates the visual percept.

A similar comparison has been made with respect to the spatial scale of interactions for binocular disparity (**Figure 5*a–c***). The vast majority of MT neurons are sensitive to the relative position of visual stimuli on the two retinas (Maunsell & Van Essen 1983b, Bradley et al. 1995, Bradley & Andersen 1998, DeAngelis & Newsome 1999, DeAngelis & Uka 2003)—a comparison essential for stereoscopic depth perception (see Cumming & DeAngelis 2001 for review)—and, indeed, MT activity has been linked to this perceptual function as firmly as it has been linked to motion perception (see below). In this case, the spatial scale of the binocular interactions in MT does appear significantly coarser than that of V1 (DeAngelis & Uka 2003) but may not be that different from the scale in V2 (Thomas et al. 2002) (**Figure 5**). Given the clustering of disparity-tuned neurons in V2 thick cytochrome oxidase stripes (Hubel & Livingstone 1987, Peterhans & von der Heydt 1993), which are known to project to MT (Shipp & Zeki 1985, DeYoe & Van Essen 1985), it is thus plausible that MT inherits its disparity tuning as well.

Overall, a number of recent studies concluded that although differences exist in some of the population properties of V1 and MT neurons with respect to direction, speed, and disparity tuning, the more carefully and quantitatively these parameters have been studied and compared, the subtler the differences have become. But this is not to say that MT simply mirrors its V1 inputs. MT is now known to be involved in a number of visual functions that are complex and, in at least some cases, are linked to perception and behavior. We discuss these functions in the following para-

graphs, starting with center-surround interactions, followed by the computation of velocity, and then operations related to segmentation and structure in three-dimensional space. We conclude with extraretinal effects and discus perceptual correlates and the mechanisms by which the MT population might be decoded by other brain centers.

SURROUND MECHANISMS

About half of the neurons in MT have receptive fields with antagonistic surrounds (Allman et al. 1985a, Tanaka et al. 1986, Raiguel et al. 1995, Bradley & Andersen 1998, Born 2000, DeAngelis & Uka 2003). These neurons respond well to a centrally placed visual stimulus, such as a small patch of moving dots; however, if the stimulus is made larger so that it invades the surrounding region, the response decreases (**Figure 6*A***).

In general, the surround effects are such that maximal suppression occurs when the surround stimulus moves in the same direction and at the same disparity as that in the center (Allman et al. 1985a, Bradley & Andersen 1998). As such, the center-surround apparatus would act as a differentiator over at least two dimensions, direction and depth, bestowing on MT firing rates the quality of salience. The more a stimulus sticks out in terms of direction and depth, the larger the neuron's response will be; in fact, the effects combine roughly linearly (Bradley & Andersen 1998). Surround suppression also depends on speed, but surprisingly, suppression is not consistently maximal when surround speed matches center speed; in fact, results have been quite mixed (Allman et al. 1985a, Tanaka et al. 1986, Orban 1997). So there may not be a simple differencing mechanism based on center-surround speed comparisons.

Although we have discussed MT surround effects in terms of direction, speed, and disparity relative to the center stimulus, effects are not relative, at least for direction and speed (Born 2000). Surround stimuli modulate the

a   **Disparity**

d   **Direction**

b

e

c

f

magnitude of responses to central stimuli but do not laterally shift tuning peaks for direction and speed. In the same way, we would expect disparity to have an absolute rather than relative effect, but we are unaware of any experiments that have tested this.

Recent data suggest that MT surrounds are actually quite complex. For example, center-surround interactions behave quite differently for low- and high-contrast stimuli: Area summation prevailed in the former case and suppression prevailed in the latter (**Figure 6*A*,*B***; Pack et al. 2005). These results are consistent with psychophysical results demonstrating improved motion integration at low contrasts (Tadin et al. 2003). The change in center-surround interactions with contrast is interesting because it points to a strategy of the visual system, first suggested by Marr (1982), to integrate for increased sensitivity when the signal is weak, but to exploit the high information content of image discontinuities by differentiating when the signal is strong. A similar effect of contrast on surround effects has been observed in both V1 (Levitt & Lund

1997, Polat et al. 1998, Kapadia et al. 1999, Sceniak et al. 1999) and the LGN (Solomon et al. 2002), so this strategy may be general.

Another level of complexity concerning MT surrounds is their spatial organization (Raiguel et al. 1995, Xiao et al. 1997a,b). The Orban lab has used small patches of moving dots to probe various positions within the surround while the center was stimulated optimally with a separate dot patch. Although about 20% of the antagonistic surrounds were circularly symmetric, 50% were asymmetric with most of the suppression being confined to a single location on one side of the preferred-null direction axis, and another 25% showed bilaterally symmetric zones of "end" suppression that tended to lie along the same axis (**Figure 6*C***). The neurons having asymmetric and bilaterally symmetric surrounds appear well suited to calculate directional derivatives of the first and second order, respectively, and computational studies have indicated that such computations are potentially useful for encoding important surface features, such as slant and tilt (first

←——————————————————————————————————————

Figure 5

Comparison of the spatial scales at which interactions for binocular disparity (*a–c*) and direction selectivity (*d–f*) are computed. Panels *a* and *d* show conventional tuning curves for a single MT cell whose receptive field was located 4.4° to the right of and 2.7° above the fovea (~5° eccentricity). This cell preferred crossed disparities (*a*) and responded optimally to motion up and to the left (*d*). Panels *b* and *e* show two-spot interaction maps for the same cell. Orange indicates facilitation, and blue indicates suppression. Panel *b* plots the probability of spiking as a function of the relative position of a probe stimulus presented to the left eye relative to the position of a simultaneously presented reference spot in the right eye (defined as 0,0 on the map). Consistent with the standard disparity tuning curve, the cell was facilitated (*orange*) by spots in the right eye appearing to the left of those in the left eye (crossed disparity) and suppressed (*blue*) by uncrossed disparities. Panel *e* plots the relative positions of the two spots on successive frames ($\Delta t = 13$ ms), revealing the facilitation for probe (*preceding*) spots down and to the right of the reference spot. For both two-spot maps, note that the relevant interactions take place over a very small spatial range. To quantify this, a gabor function was fit to the two-spot map, and the spatial frequency of the sinusoid was used as a measure of the coarseness of the interactions. For this cell, the disparity spatial frequency was 1.7 c/deg and the directional spatial frequency was 1.67 c/deg. Panels *c* and *f* show population data on the coarseness of disparity (*c*) and directional (*f*) interactions for a population of neurons in V1 and MT (and V2, for disparity). Because we did not have a large sample of disparity maps, we have used the data from figure 8 of Cumming & DeAngelis (2001). Their measure of coarseness was different from that described above; however, we believe both measures reflect the same underlying substructure. Note that, at a given eccentricity, the range of spatial scales for V1 and MT largely overlap and the interactions for MT cells are at a much finer spatial scale than the size of their receptive fields. Panels *a*, *b*, *d*, and *e* are from Pack et al. (2003); data for panel *f* are from C.C. Pack, M.S. Livingstone, B.R. Conway, & R.T. Born (unpublished observations).

Figure 6

Center-surround interactions in MT. (*A*) Effect of contrast on center-surround interactions for one MT neuron. When tested with high-contrast random dots (RMS contrast 9.8 cd/m^2) the neuron responded optimally to a circular dot patch 10° in diameter and was strongly suppressed by larger patterns. The same test using a low-contrast dot pattern (0.7 cd/m^2) revealed strong area summation with increasing size. (*B*) Population of 110 MT neurons showing the strength of surround suppression measured at both high and low contrast. Surround suppression was quantified as the percent reduction in response between the largest dot patch (35° diameter) and the stimulus eliciting the maximal response. Each dot represents data from one neuron; the dashed diagonal is the locus of points for which the surround suppression was unchanged by contrast. The circled dot is the cell from panel *A*. (*C*) Asymmetries in the spatial organization of the suppressive surround (after Xiao et al. 1997). Different kinds of surround geometry are potentially useful for calculating spatial changes in flow fields that may be involved in the computation of structure from motion. Neurons whose receptive fields have circularly symmetric surrounds (*top*) are postulated to underlie figure-ground segregation. The first- (*middle*) and second-order (*bottom*) directional derivatives can be used to determine surface tilt (or slant) and surface curvature, respectively (Buracas & Albright 1996). Panels *A* and *B* are from Pack et al. 2005.

null direction: the direction of motion opposite that eliciting the greatest response from a given neuron; e.g., if a neuron responds optimally to rightward motion, its preferred direction is right and its null direction is left.

order) or curvature (second order) (Droulez & Cornilleau-Peres 1990, Koenderink & van Doorn 1992, Buracas & Albright 1996). This potential role of the surround in structural computations is discussed further in the next section.

The source of MT surrounds remains unclear. One possibility is that the surrounds are already present in the inputs to MT. Though center-surround interactions for motion have been reported in V1 (Gulyas et al. 1987, Levitt & Lund 1997), the relative paucity of such interactions in the input layers of MT (Lagae et al. 1989, Raiguel et al. 1995, Born 2000) and the very large size of MT surrounds—at least several-fold larger than their centers (Allman et al. 1985a, Tanaka et al. 1986, Raiguel et al. 1995)—make this an unlikely explanation. It may be that surrounds reflect feedback from higher areas such as MST or are created by

horizontal connections within MT (Malach et al. 1997).

THE COMPUTATION OF VELOCITY

By "velocity" we mean the vector representation of the direction and speed of retinal motion. As discussed above, MT adds little to the raw direction and speed tuning already found in V1, but researchers still think it plays a role in computing the motion of whole objects or patterns. The nature of that role is the subject of this section. We first discuss some theoretical considerations and outline the roles MT might play.

For a rigid object, it would seem trivial to compute pattern motion because one would expect every part of the object to have the same velocity. But the measurements obtained

depend critically on how the local motion is sampled. Because of the "aperture problem," moving edges seen through small apertures appear to move orthogonally to their length; therefore, for an object sampled at high resolution (through small apertures), different parts of the object appear to move in different directions, depending on the orientation of the sampled edges (Fennema & Thompson 1979) (**Figure 7*a***). In the primate, visual motion is first computed in V1, and these neurons have small receptive fields; therefore, investigators generally think that V1 neurons see normal (orthogonal) velocities (Hubel & Wiesel 1968, Movshon et al. 1985, Heeger 1987). The problem then is to compute two-dimensional (2D) pattern motion on the basis of these local, one-dimensional (1D) samples. In theory, two local samples are sufficient to compute the pattern motion; the geometric solution to the problem is called the intersection of constraints (IOC), which is illustrated in **Figure 7*B***.

As we address below, some MT neurons report 2D motion, but the computation of 2D motion itself does not need to occur in MT; indeed, it could take place anywhere along a continuum between two extremes. At one extreme is the idea that the V1 stage is linear and the informative (nonlinear) computation occurs in MT (Adelson & Movshon 1982, Albright 1984, Movshon et al. 1985, Heeger 1987, Simoncelli & Heeger 1998). At the other extreme, 2D motion is extracted in V1 through nonlinearities, such as endstopping, and all that is required of MT is to pool the V1 inputs (Wilson et al. 1992, Barth & Watson 2000). Below, we discuss physiological evidence supporting each of these ideas. At present, there is no definitive evidence for either model, and indeed, we conclude by suggesting that both may be operative, depending on the stimulus conditions.

According to models of the first type, the aperture problem is built into the system by virtue of the linearity of the motion
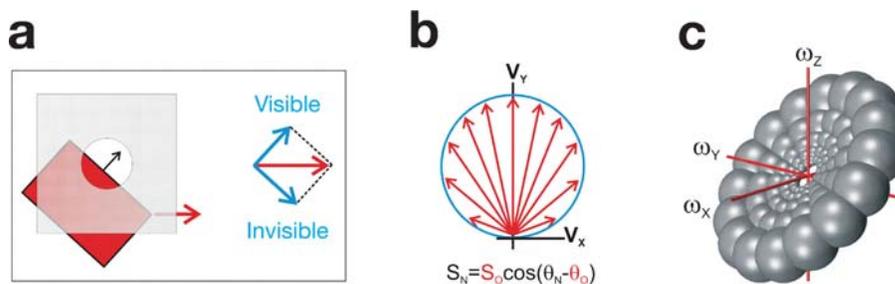
Figure 7

The problem of two-dimensional motion detection. (*A*) The aperture problem. A moving edge seen through an aperture appears to move perpendicularly to itself because the object's motion, in this case to the right, can be decomposed into vector components, one parallel to the edge and one perpendicular. The parallel component is invisible because there is no contrast parallel to an edge, so only the perpendicular component remains. (*B*) The relationship between the component (apertured) vector samples and the global motion of an object is cosinusoidal; that is, the speed of the samples is the object speed times the cosine of the difference between the object direction and the direction of the vector sample, as shown in the equation. In the equation, S_N and θ_N are the normal (sampled) speed and direction, and θ_O and S_O are the speed and direction of the object. Because there are two unknowns, the object direction and speed (*shown in red in equation*), two samples are needed to solve for the object velocity. This requirement is usually referred to as the intersection of constraints (IOC). It is often visualized differently (Movshon et al. 1985). (*C*) A possible neural algorithm for solving the IOC, as suggested by Simoncelli & Heeger (1998). For a rigid, translating object, all local spatiotemporal frequencies must lie on a plane in frequency space. To detect this, one could create a linear filter, represented by blobs in the diagram, for each location on the plane, then sum the energy passed through the filters.

detection stage of V1 simple cells. Consider the frequency representation of moving objects (Watson & Ahumada 1983). For any rigid moving object, the spatiotemporal frequency of all local samples must lie on a plane in frequency space (**Figure 7c**). V1 simple cells, to a first approximation, act like linear space-time filters (McLean & Palmer 1989, Reid et al. 1987), and complex cells are thought to differ mainly in their phase-insensitivity but not in their frequency selectivity (Movshon et al. 1978). So V1 neurons effectively measure the amount of motion energy in their passband (Adelson & Bergen 1985). In other words, such neurons do not really know what the stimulus direction is; they see only the motion component within their frequency band. This is the expression of the aperture problem in frequency space (see **Figure 8**).

If V1 neurons see component motion, they are ignorant, in a sense; MT neurons would need to be relatively intelligent in combining V1 inputs to recover the true, 2D direction of motion. As described above, the IOC construction is the basic rule needed to compute pattern velocity from component (local) velocities. But what physiological mechanism could do this? Heeger (1987) and Simoncelli & Heeger (1998), building on important theoretical (Adelson & Movshon 1982, Watson & Ahumada 1983, Movshon et al. 1985) and physiological (Hubel & Wiesel 1962, Movshon et al. 1985, Reid et al. 1987) groundwork, described what we refer to as the F-plane model. It assumes a front end made of linear V1 cells whose outputs are summed over a plane in frequency space by an MT pattern cell. This planar summation is an instantiation of the IOC rule (**Figure 7C**). The model is able to explain a number of physiological results, including MT responses to variable coherence stimuli (Newsome et al. 1989) and to plaid patterns (Adelson & Movshon 1982). There are other important models of MT computation, however, which we regrettably do not have space to discuss here (Wilson et al. 1992, Nowlan & Sejnowski 1995, Lisberger & Movshon 1999).
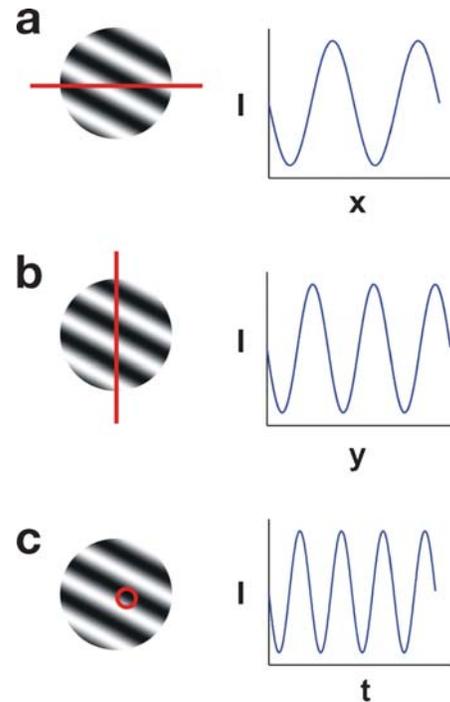
Figure 8

Cutting a horizontal slice through an oblique sine wave grating reveals a sinusoidal modulation of intensity vs. x position (*A*). Cutting a vertical slice through the same grating reveals an identical intensity modulation versus y position (*B*). Looking at a fixed location as the grating moves reveals a sinusoidal modulation of intensity versus time (*C*). Changing the angle (direction) of the grating changes the relative x and y sinusoidal frequencies, and changing the grating speed changes the temporal frequency. Thus, the velocity (direction and speed) of the grating is completely characterized by a single, three-dimensional frequency, (ω_x, ω_y, ω_t). Just as any sound is the sum of its harmonics, any moving object can be represented in terms of its component frequencies, each equivalent to a single, moving sinusoidal grating. If the object is rigid and not rotating, all of its component frequencies will lie on a plane in ω_x, ω_y, ω_t space. The aperture "problem," stated in these terms, arises insofar as V1 neurons are linear ω_x, ω_y, ω_t filters, each detecting a certain component frequency. The relative blindness, or ignorance, implied by the aperture problem is in the linearity of these cells; they are presumably unaffected by frequencies outside their passband. Thus, the "component" cells of Movshon et al. (1985; see text) see only one grating—one frequency.

Note that even if V1 neurons act like linear filters, MT neurons might not necessarily combine their outputs according to an IOC rule; a vector average or sum, for example, would also be a plausible combination (Mingolla et al. 1992, Wilson et al. 1992, Rubin & Hochstein 1993).

An alternative to the F-plane model is that 2D-motion information is computed in V1 through specific nonlinear operations. For example, image squaring can be used to extract periodic elements, which can be low-pass filtered from component frequencies (Wilson et al. 1992), and luminance minima and maxima are reliable features to track, as well (Bowns 1996). We see below that endstopping in V1 neurons amounts to feature detection, which has been formally related to the more general notion of curvature (Barth & Watson 2000). Because features always move in the object direction and at the object speed, MT would not really need to elaborate on V1's output, other than perhaps spatial pooling and noise reduction. At this stage, we cannot rule out that such pooling is the only role played by MT in pattern motion detection.

Having outlined the different possible computational mechanisms, we now discuss evidence for and against them. The first breakthrough came from experiments by Movshon and colleagues (1985), who tested MT and V1 neurons with stimuli known as plaids. These stimuli were formed by superimposing two sine gratings moving in different directions, in this case 135° apart. Treating the summed gratings as a single, plaid stimulus, they measured direction tuning in MT neurons and found a continuum of different tuning curves. At one extreme, there were two peaks in the direction tuning curve, corresponding to the two-pattern directions that resulted in one of the gratings moving in the neuron's preferred direction. At the other extreme, the tuning curve was unimodal, peaking where the pattern as a whole moved in the neuron's preferred direction. Movshon and colleagues (1985) coined the terms pattern and component cell to represent these two

types of response. They found that 25% of the MT neurons yielded tuning curves significantly more like the pattern response and 40% more like the component response; the remaining 35% of the neurons were unclassified. In V1, nearly all of the cells displayed component behavior, and none matched the pattern prediction. These authors roposed a two-stage mechanism where pattern cells combine the outputs from component cells to compute pattern direction and suggested the possibility of an IOC construction. Because the plaids were symmetric, the direction of the IOC and the direction of a vector average (for example) would come out the same, so these experiments did not prove the operation of an IOC mechanism.

However, Albright showed that for some MT neurons, which he called Type II cells, the preferred orientation of a static bar was parallel to the preferred direction of motion (Albright 1984). This behavior is consistent with the IOC rule because the vector component 90° off the object direction has zero speed (see **Figure 7b**). These Type II cells were later shown to correspond to Movshon et al.'s pattern cells (Rodman & Albright 1989). Other studies have found evidence that MT pattern cells are bimodally tuned for bars (Okamoto et al. 1999) and gratings (Simoncelli et al. 1996). The IOC model predicts this also, assuming the stimulus is moving beneath the neuron's preferred speed. In that case, the neuron should have two preferred directions, one for each time the stimulus crosses the cosine-shaped function relating direction to speed (see **Figure 7b**). Unfortunately, both studies were based on small samples.

Other evidence suggests that a two-stage model may not be required because the aperture problem is overcome in V1. Layer 4B neurons, which dominate the V1 input to MT, are heavily end-stopped, typically exhibiting around 75% suppression by extended contours as compared with their maximal response (Sceniak et al. 2001). This effect is largely independent of the orientation of the stimulus in the surround; therefore, these

neurons respond well to line terminators moving in their preferred direction, regardless of the orientation of the contour (Pack et al. 2003). Although not tested directly, these cells likely show a similar preference for corners, dots, and other features compared with extended contours. Because features always move in the object direction, and because end-stopping suppresses neurons not responding to features, end-stopping tends to have the important effect of defeating the aperture problem. Whether end-stopping actually produces a pattern-motion computation in the naturally functioning visual system remains to be seen.

But some evidence suggests that end-stopping does play a critical role in solving the aperture problem. Pack & Born (2001) tested MT neurons with a pattern of line segments drifting coherently such that the motion components—the velocities normal to the segments—differed by 45° from the direction of the pattern as a whole. The neuronal responses were initially strongly biased by the component directions and then evolved to the pattern direction over the course of about 80 ms. In a separate study of V1 neurons, the end-stopping effect was shown to also develop over a similar time course (Pack et al. 2003). Thus, MT neurons may have computed the motion of the line pattern by integrating the output of a feature-based mechanism afforded by end-stopping in V1.

But the slow time course observed in MT by Pack & Born does not need to reflect end-stopping in V1. Smith et al. (2005) recently measured the time course over which MT neurons develop pattern selectivity and also found it to be gradual. Because they used sine wave plaids, the observed time course may have had nothing to do with end-stopping, reflecting instead mechanisms within MT or even top-down effects. Of course, one could argue that the overlap regions of the plaids constitute features that could be tracked by end-stopped (or other feature-selective) neurons; in that case, though, one would expect to find pattern cells in the V1 inputs to MT. Movshon & Newsome studied this in 12

MT-projecting V1 cells and did not find any (Movshon & Newsome 1996), but this sample may be too small to tell. Only 9 of these cells were tested with plaids, and only 6 of the 12 cells were in layer 4B. Because 90% of MT's V1 input comes from 4B, it is premature to conclude that the V1 cells feeding MT do not have pattern behavior. In fact, Tinsley et al. (2003) and Guo et al. (2004) both found a small number of pattern-selective cells in V1. Clearly, the issue of whether substantial pattern selectivity occurs in primate V1 remains unresolved. Still, under conditions where Movshon et al. did not find V1 pattern cells, they did find MT pattern cells (Movshon et al. 1985); therefore, the pattern mechanism under those conditions cannot be explained solely in terms of feature tracking.

In summary, there is substantial evidence for both feature tracking in V1 and a two-stage mechanism involving linear filtering in V1 followed by a nonlinear process, something like IOC or vector averaging, in MT. We note that IOC and feature tracking mechanisms are not necessarily incompatible; in fact, there is perceptual evidence that different sorts of computation are at play under different circumstances (Weiss et al. 2002). In the absence of end-stopping, V1 neurons are assumed to extract motion energy at the various spatiotemporal frequencies in the stimulus. For the F-plane model to be robust, it is best to have energy broadly distributed over the frequency plane defined by the object's velocity; otherwise, it is difficult for the MT population to determine the orientation of this plane. This may be why sinusoidal plaid stimuli, whose energy occupies only localized portions of the frequency plane, are not perceived as moving in the IOC direction unless the grating directions are roughly symmetric about the pattern direction (Yo & Wilson 1992). When end-stopping is operational, neurons with extended contours in their receptive fields are suppressed; so the remaining input consists mainly of features that have energy that is well dispersed over the frequency plane. Therefore, the overall effect

would be to provide MT with a well-balanced, broad-spectrum input. At low contrast, where end-stopping becomes weak or even nonexistent (Sceniak et al. 1999), the system would revert to a more linear mode of operation, using signals derived from moving contours as well as features. The idea of representing moving objects in terms of sparse features at high contrast and diffuse frequency components at low contrast is consistent with theoretical studies demonstrating the advantage of minimizing redundancy when signal-to-noise is large, and at the same time it emphasizes sensitivity and noise reduction using broad pooling mechanisms at low contrast (Field 1987, van Hateren 1992). Of course, other nonlinear mechanisms besides end-stopping could also be used to track features (Wilson et al. 1992, Bowns 1996).

NOISE REDUCTION

Regardless of how pattern velocity is computed, the visual motion system is compelled at some point to filter noise from the processing stream. MT neurons appear to serve this function in a way that is akin to common mode rejection by a differential amplifier (Snowden et al. 1991, Qian & Andersen 1994, Qian et al. 1994, Bradley et al. 1995). Snowden et al. showed that MT neurons responding to dot patterns moving in their preferred direction were suppressed when dot patterns moving in nonpreferred directions were simultaneously introduced (Snowden et al. 1991). This suppression, termed motion opponency, is not a guaranteed result; V1 neurons, for instance, are not substantially affected by nonpreferred motion directions, consistent with their approximately linear behavior (Qian & Andersen 1995). Snowden et al. demonstrated that nonpreferred motions exhibited a suppression in MT that was roughly divisive; that is, the nonpreferred pattern tended to reduce the response gain for the preferred-direction pattern. Later studies by Qian & Andersen showed that suppression of MT by nonpreferred directions is particularly strong

when opposing motions occur within ∼0.5° of each other, roughly the scale of V1 receptive fields (Qian & Andersen 1994). The fact that V1 cells do not themselves show appreciable motion opponency suggests that there is strong mutual inhibition at the stage of V1 inputs onto the dendrites of MT neurons. Because a flash emits motion energy simultaneously in all directions, a mechanism that cancels opposite-direction signals on a local scale could be a particularly effective way of reducing responses to flicker.

There is no reason to assume that the only function of motion opponency in MT is to reduce noise. In fact, opponency is likely at least partly a manifestation of gain normalization, the process by which neural responses are scaled according to the total amount of neural activity in their immediate vicinity (Simoncelli & Heeger 1998, Heuer & Britten 2002). But there is little doubt that opponency would tend to reduce the responses to motion noise. Some behavioral evidence also exists: Perceptual studies in a patient with bilateral damage to a region corresponding to MT/V5 found that performance was normal for various motion tasks except when noise was added to the stimulus, in which case performance fell to chance (Zihl et al. 1983, Marcar et al. 1997). This, together with the suppressive effects of nonpreferred motion discussed above, suggests that MT has a basic role in noise reduction within the motion processing stream.

SEGMENTATION

Although pooling is an important stage in motion processing, it introduces its own problems. It is not uncommon for more than one moving object to appear in the same part of visual space, and pooling these movements would obviously be inappropriate because there is nothing meaningful about the joint (say, average) velocity of two independent objects. Therefore, pooling mechanisms need to be accompanied by parsing mechanisms that distinguish groups of

signals to be integrated separately (Nowlan & Sejnowski 1995, Hildreth et al. 1995).

Several lines of evidence suggest that MT neurons are equipped with response properties that allow them to carry out, or at least contribute to, this parsing. For one thing, the suppression of MT responses normally exerted by nonpreferred motion is relaxed when the nonpreferred and preferred motions occur in separate depth planes (Bradley et al. 1995). Opposing movements in the same part of 2D visual space usually are separated in depth (otherwise they would collide), which would tend to prevent the pooling and cancellation of motion signals emanating from different objects. Also, most MT neurons have an antagonistic surround that is least suppressive under conditions where center and surround stimuli move in different directions and speeds and at different stereoscopic depths (See Surround Mechanisms). This could be a mechanism for emphasizing the relative motion of an object against its background. Other studies suggest that more complex mechanisms may be in place. For example, Albright and colleagues superimposed square wave gratings and manipulated the luminance at the overlaps, according to physical transmittance rules, to produce stimuli that looked either transparent (separate gratings) or coherent (single plaid) in their static state. They then demonstrated that single MT neurons could exhibit either pattern- or component-like direction tuning, depending on whether the stimulus was in its coherent or transparent configuration, respectively (Stoner & Albright 1992, Stoner & Albright 1996). These results could reflect external parsing mechanisms that influence MT, but they could also reflect low-level mechanisms where the overlap regions of the plaids are detected by nonlinear mechanisms in V1, leading to a change in the distribution of inputs to MT. Finally, MT neurons are better able to extract signal (motion) from noise when the two have different isoluminant colors (Croner & Albright 1997, 1999). All together the evidence rather strongly suggests

that MT neurons are critically involved in segmenting an image into separately moving parts.

THE COMPUTATION OF STRUCTURE

One of the most important discoveries since MT was first located was the binocular disparity tuning of its neurons. Maunsell & Van Essen (1983a) showed, using stereoscopic moving bars, that a majority of MT cells were disparity selective, although it is now known that moving dots, which have a broader frequency content, reveal selectivity in almost all MT cells. The tuning resembles sigmoids, Gaussians, and shapes in between. Curves sometimes peak near zero disparity, but usually they peak or flatten out well to the left or right. Therefore, with some exceptions, these neurons are tuned "near" or "far," with about a twofold preponderance of the near-tuned (Bradley & Andersen 1998). Importantly, Maunsell & Van Essen showed that MT neurons are not tuned for motion through 3D space. They are simply tuned for a certain 2D direction in a plane a certain distance from the fixation point. This remained something of an anomaly until the mid-1990s when experimenters began searching for possible functions of disparity in MT. First, they showed that null-direction motion, which normally suppresses MT activity, becomes less suppressive if it occurs outside the preferred depth plane of the neuron. The suppression is itself thought to have a role in noise reduction, so this depth constraint provides a way of confining the filtering mechanism to a particular surface. Later it was shown that surround inhibition is also modulated by disparity, predictably in such a way as to minimize inhibition when the surround stimulus is outside the depth plane containing the center stimulus (Bradley & Andersen 1998). This could be a mechanism for segmenting an object from its background. So there is some evidence that disparity is wired into MT in a way that facilitates the processing of

visual motion, presumably for purposes of noise reduction, segmentation, and probably other functions.

However, subsequent studies suggested that MT is involved in the perception of depth itself (Bradley et al. 1998, DeAngelis et al. 1998, Dodd et al. 2001). Two groups of investigators trained monkeys to view revolving cylinders whose direction of revolution was unspecified in the stimulus, but which nevertheless appeared to rotate (**Figure 9**). The perceived rotation was bistable, and monkeys reported their percept on each trial. Both groups found a clear correlation between MT firing rates and the monkeys' judgments. In terms of motion, both percepts meant seeing two, opposite directions; the only difference was the order of these directions in depth. So these were the first neural correlates of the perception of depth. In fact, Dodd et al. (2001) computed choice probability, a measure of the correlation between perception and neural activity (Britten et al. 1996), and found the strongest neuro-perceptual correlation of any MT study, to date.

This role for MT in depth perception has only been strengthened by additional experiments. In fact, of the criteria linking neurons to perception proposed by Parker & Newsome (1998), the only important one that has yet to be met is that of MT lesions affecting disparity judgments. Thus far, this research has rigorously demonstrated (*a*) neuronal selectivity for disparity (Maunsell & Van Essen 1983b, DeAngelis & Uka 2003), (*b*) neuronal disparity sensitivity that is sufficient to account for the abilities of monkeys to perform coarse disparity discrimination tasks (Uka & DeAngelis 2003), (*c*) a predictive relationship between MT neuronal activity and monkeys' perceptual decisions concerning depth (Uka & DeAngelis 2004), and (*d*) the ability to predictably bias monkey's disparity judgments by microstimulation of disparity columns favoring a given depth (DeAngelis et al. 1998).

Another hint that MT neurons may be involved in the extraction of surface

Orthographic projection

properties is the presence of inhomogeneities within the receptive field with respect to tuning for both speed (Treue & Andersen 1996) and binocular disparity (Nguyenkim & DeAngelis 2003). As a moving textured surface in the fronto-parallel plane is either tilted forward or backward or slanted to the right or left, the retinal projection of local motion and depth vectors will form a gradient in both speed and disparity. If MT neuronal receptive fields possessed systematic variation in these tuning properties as a function of position within their receptive fields, the resulting structure might serve as a template for a particular 3D surface orientation. Indeed, both of the above groups have demonstrated tuning for surface orientation on the basis of either cue alone. The group testing speed gradients confined their stimuli to the receptive field center, but it appears that, if asymmetries of the surround described above are included, the tuning to speed gradients may become even more marked (Xiao et al. 1997a). Furthermore, it now appears that at least some MT neurons are selective for surface orientation defined by both cues. In such cases, the selectivity is generally consistent and reenforcing, in that tuning is sharper to gradients defined by the combination than by gradients defined by either cue alone (Nguyenkim & DeAngelis 2004).

Figure 9

Schematic illustrating cylinder experiments first used to link depth perception to MT. A monkey views the orthographic projection, or shadow, of dots revolving on a transparent, cylindric surface. The planar image contains only dots moving in opposite directions, but the observer perceives a three-dimensional revolving cylinder. Monkeys are trained to report the perception of structure (Siegel & Andersen 1988) or the direction of revolution (Bradley et al. 1998, Dodd et al. 2001).

EXTRARETINAL EFFECTS

For most behavior, visual information must be integrated with other, nonvisual information. An example of this is the use of copies of the signals used to generate eye movements, so-called efference copy or corollary discharge, to aid in disambiguating retinal motion caused by the eye movements themselves from that due to motion of an object. In ascending the hierarchy of visual areas, at least in the dorsal stream, such extraretinal influences tend to become increasingly powerful. Thus, whereas investigators have reported small-to-modest effects of eye position (Bremmer et al. 1997), saccadic eye movements (Thiele et al. 2002), and attention (Treue & Maunsell 1996) for some MT neurons, much larger and more prevalent effects of these signals have been found in areas above MT, particularly MST and LIP. So, at least to a first approximation, MT is a relatively faithful representation of events occurring on the retina.

The issue of extraretinal influences in the dorsal stream was first examined by Wurtz's group at the National institutes of Health (NIH) in the context of smooth-pursuit eye movements (Newsome et al. 1988). MT neuronal signals are important for the initiation of pursuit (see Lisberger et al. 1987 for review), and many MT neurons with foveal receptive fields are also active during ongoing pursuit. However, when Newsome et al. (1988) eliminated retinal motion, either by briefly extinguishing the target or by using the recorded eye movements to stabilize the target's image on the retina, the MT responses disappeared. This result stood in marked contrast to many neurons in MST that showed continued directional responses under the same conditions.

Subsequent groups have found some tendency for the position of the eye in the orbit to affect the overall level of responsiveness of some MT neurons, without affecting their tuning for direction (Bremmer et al. 1997). But, in line with the idea of hierarchy, the effects in MT were both rarer and smaller in magnitude than those found in MST, one of the next higher-tier motion-processing areas to which MT projects. And it is telling that this type of effect was initially discovered in an area still further up the hierarchy—7a of posterior parietal cortex (Andersen et al. 1985), where the effects of eye position are even more profound and where vestibular, auditory, and somatosensory information is also integrated (Andersen et al. 1997). None of these latter signals are known to influence neurons in MT, and anatomical data would suggest they are unlikely to do so.

Perhaps the most prevalent nonretinal influence on MT neurons is that of attention. This is manifest as an enhanced neuronal response to visual stimuli when an animal is attending to either the spatial location of the neuron's receptive field (Seidemann & Newsome 1999, Treue & Maunsell 1999) or to some preferred neuronal feature, such as a particular direction of motion (Treue & Martinez-Trujillo 1999). The gain increase appears to be a straightforward multiplication of the responses, without any changes in the shape of the direction tuning curve (Treue & Maunsell 1999) nor in the nature of the underlying motion computations (Cook & Maunsell 2004). However, the magnitude of the gain may change both as a function of stimulus contrast (Martinez-Trujillo & Treue 2002) and, for feature-based attention, as a function of the similarity between the attended feature and that preferred by the neuron, actually becoming negative as the attended feature approaches the antipreferred feature of the neuron (Martinez-Trujillo & Treue 2004). As for other extraretinal effects, however, the general magnitude of attentional modulation in MT appears to follow the cortical hierarchy: Attentional modulation strengths range from less than 10% in V1 (McAdams & Maunsell 1999), to a ballpark figure of 20%–30% in MT (Treue & Maunsell 1999), to values well over 50% in higher-tier areas, such as MST and 7a (Maunsell & Cook 2002).

PERCEPTUAL CORRELATES AND POPULATION CODES

Single-Neuron Sensitivity

In classic experiments at Stanford University, Newsome and colleagues trained macaques to watch moving dot patterns and then indicate which of two opposite directions they had seen (see Parker & Newsome 1998 for review). The strength of the motion signal was controlled by varying the fraction of dots moving coherently, and the remaining dots moved in random directions. The task was executed simultaneously with the recording of single MT neurons, in each case aligning the coherent motion axis with the preferred direction of the recorded neuron. Using methods from signal detection theory, Newsome and colleagues were able to compare neuronal sensitivity directly with that of the monkey itself. Remarkably, they discovered that most MT neurons were at least as sensitive as the monkey itself. Later, the same group defined the choice probability (CP), an extension of detection theory, which reflects the correlation between a subject's judgments and random fluctuations in a single neuron's firing rate. For their task, the mean CP in macaques was only 0.55; chance was 0.50 and perfect correlation was 1. In a computational analysis, Shadlen et al. (1996) concluded that roughly 70–100 neurons would have been involved in the decision pool for the task, far more than would seem necessary considering the exquisite sensitivity of single cells.

Shadlen et al. (1996) suggested several possible reasons for the discrepancy, including correlated noise in MT's inputs, which would limit the benefits obtained by pooling, noise in downstage decision processes, and the likelihood that, owing to limitations in the precision of cortical connectivity, signals from relatively insensitive neurons would also be included, thus degrading the calculation. But this coarse pooling may not occur under all conditions. For example, a recent study at

the University of Chicago showed that when monkeys performed fine direction discrimination, neuronal sensitivity was at best 2–3 times worse than the observer as a whole, and no amount of pooling could account for the psychophysical data unless the most sensitive neurons were selectively pooled (Purushothaman & Bradley 2005). The different results obtained by the two groups probably reflects important differences in the tasks they used. The Stanford task used a large direction difference embedded in noise, whereas the Chicago stimuli were noise-free but the monkeys had to discriminate very small direction differences. One would expect the former task to reflect the sensitivity and filtering capability of the neurons, whereas the latter task should depend more on the slopes of the direction tuning curves. Of course, both tasks probe critical aspects of MT processing. The point is that a neuron's sensitivity relative to the observer is likely to depend on the task, and in particular the computational role the neuron plays in the decision process.

Other examples reinforce this idea. Uka & DeAngelis (2004) trained monkeys in a near/far-depth-judgment task and compared their sensitivity with that of MT neurons. In each case the near and far depths were set at the worst and best values for the MT cell being studied, much like testing a neuron with its preferred and antipreferred directions. Though depth differences were large, the task was made difficult by adding noise to the stimulus. They found that single neurons were on average as sensitive as the observers. In contrast, Liu & Newsome (2003a, 2005) trained monkeys to discriminate small speed differences and found that MT neurons were much less sensitive than the observers. Overall, it would seem that single MT neurons are exquisitely sensitive when the task is to detect a large direction or disparity difference that is heavily corrupted by noise, but they are less sensitive (relative to the observer) when the task requires fine discrimination

of the relevant cue (e.g., direction or speed).

Yet another important factor in interpreting such studies is the role of temporal integration. The Stanford experiments used stimulus presentation intervals of two seconds, after which time monkeys indicated their decision. If the monkeys actually made their decisions much earlier, however, this could affect the ratio of neuron-to-observer sensitivity because the signal detection analysis used the entire two seconds to compute neuronal sensitivity (Mazurek & Shadlen 2002). Cook & Maunsell (2002) found some support for this idea in monkeys trained in a reaction time task with variable-coherence stimuli. When integration times were commensurate for neurons and observers, the neuronal sensitivity was found to be substantially less than observers. Some caution is warranted, however, because the task was not identical to that used in the Stanford experiments. In contrast, Britten et al. (1992) showed that psychophysical and neural thresholds declined similarly with shorter stimulus presentations, which would produce similar neuron/observer-sensitivity ratios regardless of the particular time window chosen. Uka & DeAngelis (2004) also found a similarly small effect of integration interval on neuronal sensitivity in their disparity task, probably because of serial correlation (Osborne et al. 2004). Overall, the bulk of the evidence suggests that observers probably do make decisions in less than two seconds, and that information continues to accumulate for two seconds in spike trains, assuming it is extracted with the type of signal detection analysis used in the detection and discrimination experiments discussed above. That said, the effects probably are not dramatic, and the basic claim of the early Stanford experiments, that monkeys could perform the task in question with a relatively small number of neurons—compared with the hundreds or thousands of neurons one might suspect—is probably correct.

Vector Summation versus Winner-Take-All

For any simple moving stimulus, the response distribution in MT assumes a roughly Gaussian shape. By "simple" we mean that the stimulus is translating, rigid, and not rotating; by "distribution" we refer to the mean firing plotted on the ordinate versus the preferred direction of the neurons on the abscissa. Under the same visual circumstances that create such a distribution in MT, subjects accurately perceive the direction of the moving stimulus. Given the mountain of evidence linking MT to direction perception, we seek to determine how the response distribution is linked to the direction perception. More formally, we recognize that the response distribution is characterized by many numbers—the firing rates of many neurons—but the perceived direction is a single number. So there must be a code, a rule, for the conversion of many to one. But what is it?

Two simple possibilities come to mind. First, the direction percept may derive from the peak of the distribution; that is, the preferred direction of the most active neurons is taken by decision networks as the direction signal. Second, the overall distribution mean could constitute the direction signal. The Newsome lab has also attempted to probe these two potential mechanisms using microstimulation (Groh et al. 1997, Nichols & Newsome 2002). The basic experiments involved a moving visual target paired with the electrical stimulation of neurons tuned to a different direction, and animals were required either to pursue the visual target or to report simply the direction of motion they perceived. The authors' rationale was that if direction percepts derive from activity peaks, then the animals' answers should center on either the direction of the visual target or the direction encoded by the stimulated neurons. In comparison, if direction percepts depend on the activity distribution as a whole, then the perceived direction should lie somewhere in between. The general finding of these

experiments was that direction percepts are usually somewhere between the two extremes, suggesting that direction percepts derived from pooled activity rather than from activity peaks. But a potential confound in these experiments is that animals might have perceived two directions at one time. Forced to choose a single direction, they may have settled on a strategy of splitting the difference. There is, however, no evidence for this.

Besides the winner-take-all and vector-average hypotheses, Weiss et al. (2002) have proposed a Bayesian model of motion perception, which could be implemented with appropriate weighting of MT responses. Unlike vector-average and winner-take-all schemes, the model would address the MT response distribution probabilistically; as such, it could take into account the effects of noise on uncertainty and allow the introduction of priors (biases). The model can explain a remarkable array of psychophysical observations, so it will be interesting to test the model with MT recordings as well.

Distributed Speed and Acceleration Codes

Maunsell & Van Essen (1983b) found that MT cells were generally broadly speed tuned but, by and large, tended to have distinct preferred speeds. Lagae et al. (1993) later distinguished MT neurons in terms of their speed tuning as being low-pass, high-pass, or bandpass. Because high-pass neurons generally increased firing as stimulus speed increased, they pointed out that the overall mean activity of these cells could be used to gauge the stimulus speed. Recently, both Churchland et al. (2001) and Priebe & Lisberger (2004) found that speed percepts in macaques were consistent with the firing rate-weighted average preferred speed of MT neurons. Lisberger & Movshon (1999) successfully used a similar population average to account for changes in stimulus speed in anesthetized monkeys. Because the population average can shift only if single neurons change their ac-

tivity, one would expect MT firing rates to correlate with speed judgments. Indeed, preliminary evidence suggests that they do (Liu & Newsome 2005).

Lisberger & Movshon (1999) studied MT responses to accelerating random dot patterns. Judging from the neurons' sustained firing rates, there was no evidence for single-neuron encoding of acceleration. However, using a measure of the neurons' transient responses and taking their weighted average, the authors could accurately predict the target's acceleration. This result was important not only because it was the first evidence for acceleration coding in MT, but also because it revealed a signal quite hidden in the population response. One wonders how many other kinds of information are encoded in such distributed forms.

CONCLUSIONS

Cortical physiologists often claim—whether or not it is true—that in studying a particular area they hope to discover general principles of cortical function. One could argue that more information has been learned from MT than from any other visual area. We make this bold claim because MT has, in many ways, disappointed its explorers, who initially expected a number of obvious contributions to motion processing but did not find them. Although MT may slightly extend motion detection to longer ranges and higher speeds, these are clearly not its main functions; nor does it make the obvious step from speed tuning (as in V1) to acceleration tuning, at least in single neurons. So it is a testament to the persistence and ingenuity of researchers in the field that visual motion research has reexamined itself and reapproached the study of MT in a variety of novel and fruitful ways. These new approaches and their results have been the focus of this review.

Overall, MT does not appear to detect or measure visual motion; this computation occurs in V1. It also does not elaborate substantially on this basic signal; for example,

BDA: biotinylated dextran amine

FEF: frontal eye field

LGN: lateral geniculate nucleus

LIP: lateral intraparietal area

MT: middle temporal area

MST: medial superior temporal area

MSTd: dorsal subdivision of MST

MSTl: lateral subdivision of MST

PIP: posterior intraparietal area

SC: superior colliculus

V1: primary visual cortex, striate cortex or area 17

V2: second visual area

V3: third visual area

V3A: V3 accessory area

V4: fourth visual area

V5: MT

VIP: ventral intraparietal area

VP: ventral posterior area

direction tuning is not much sharper in MT, and speed tuning is not much broader. One of MT's main functions—that is, above and beyond what is done in V1—concerns integration and segmentation. Obviously, its large receptive fields combine information over space, and it integrates V1 inputs and combines them, at least under some conditions, to compute pattern motion. Its opponent mechanisms probably have a noise-reducing effect. But with integration, new problems arise, in particular, the inappropriate merging of independent moving objects. MT appears to have built-in mechanisms to deal with this. For example, opponency has a disparity constraint, and possibly other constraints, to limit integration to a particular depth. And the center-surround apparatus is direction- and disparity-constrained in such a way that neurons tend to segment motion from its background.

The idea that MT deals only with segmentation and integration might have sufficed up until the mid 1990s, but since then, a series of remarkable studies has made it clear that MT is involved in the computation of structure (although the first evidence for this fact dates back to Siegel & Andersen 1988). The sensitivity of MT neurons to speed gradients; the correlation between MT responses and the perception of 3D cylinders; and the remarkable integration of direction, speed, and disparity gradients all make a compelling case that MT is processing motion but doing more than computing the direction and speed of motion.

One of the important, largely unexplored questions about MT is how its population response is read out for different tasks. Several studies have addressed this question; however, there are many ways to decode a population (Seung & Sompolinsky 1993, Weiss et al. 2002, Ben Hamed et al. 2003), and many experiments will be required before we understand the mathematics between MT activities and downstream behavior. Because its response properties are well understood and because of its tight links to perception, MT is an ideal place to evaluate models of population decoding.

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