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scribed, but the nouns were the real ones that the mothers had used. These subjects guessed the target verbs correctly over 80% of the time, though they saw no scenes. This result reveals that the nouns co-occurring with a verb can add significant information about its meaning if the syntactic positioning (and, hence, the semantic role) of these nouns is known. Knowing that *ice cream* and *hamburger* occurred "somewhere" in the mother's utterance (as in the second condition) is not too informative: After all, the sentence might be "Ice cream ruins your appetite" or "The hamburger fell on the floor." But knowing that these "edibles" occurred as the direct object of the mystery verb is a good clue that it might mean 'eat.'

We conclude that structural information is a requirement for efficient verb learning. The frame ranges provide strong cues to interpretation. In the presence of this structural information, the complement selection (the syntactically positioned nouns) provides significant further clues. In contrast, the set of scenarios taken alone—or even taken in combination with (asyntactic) knowledge of all co-occurring words—leaves too much latitude to allow verb identification.

All in all, our work suggests that verbs' meanings cannot be extracted by a procedure that pairs single words to their observational contingencies. This is because verbs do not as a rule directly encode actions and events. If they did, grunting and pointing could substitute for elaborate human language systems. Instead, verbs encode acts and states of the world and of the mind under particular (and invisible) stances toward these adopted by the speaker. A further data source is therefore required to rein in the hundreds of salient interpretive choices made available by perception and pragmatic inference as to the speaker's intent. It is the infant's natural appreciation of syntactic structure

and its mapping onto conceptual structure that provides this additional data source.

**Acknowledgments**—This work was supported by a grant to L.R. Gleitman from Steven and Marcia Roth, whose aid we acknowledge with gratitude.

## Notes

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# Neural Foundations of Visual Motion Perception

J. Anthony Movshon and William T. Newsome

The detection and analysis of motion is one of the fundamental tasks of vision, because practically everything of interest in the visual world moves. Although motion analysis of a high order is evident in such simple visual systems as the fly's, it is only in primates that a well-defined anatomical division of the central visual pathways can be seen to be specialized for the analysis of motion.<sup>1</sup> The best defined area in this pathway is an extrastriate area known as MT (or V5). Unlike other areas of the monkey's extrastriate visual cortex, almost all neurons in MT are direction selective, meaning that they typically respond best to motion within a given range of directions, and respond not at all (or with inhibition) to motion in the opposite direction. The activity of MT neurons

has been linked to a variety of motion-related tasks, including the analysis of the motion of complex patterns, the detection of target motion relative to the background, and the generation of signals for smooth pursuit eye movement.<sup>2</sup>

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In this review, we discuss recent evidence from our laboratories that allows us to infer with unique clarity the role that MT plays in conveying the signals that support the detection and discrimination of motion. We have devised a special stimulus to isolate signals arising in motion-sensitive mechanisms, and shown that small lesions of MT specifically disrupt the ability of monkeys to discriminate motion in this stimulus. We have shown that the activity elicited in MT neurons by this stimulus, when suitably analyzed, reveals them to carry signals capable of supporting monkeys' perceptual performance. Finally, we have shown that electrical microstimulation of small groups of MT neurons alters monkeys' perceptual judgments of motion in a manner predictable from the properties of the neurons stimulated. We conclude that the activity of neurons in MT is both necessary and sufficient to account for monkeys' motion-detection performance, and that modifying this activity can modify animals' perceptual judgments of motion.

We have recently reviewed this evidence in somewhat greater detail.<sup>3</sup>

### A STIMULUS TO ISOLATE MOTION-SENSITIVE MECHANISMS

To probe the functions of the visual motion system, we tried to create a visual task that would require the selective response of motion-sensitive visual mechanisms. We wished to use a stimulus in which the *only* cue available was a motion cue, separated from confounding factors such as a change of feature position, or a change in overall temporal or spatial structure. The stimulus we devised consists of a large number of randomly positioned bright dots presented on the face of a

CRT screen. When no coherent motion signal is present, the dots are presented in a rapid random stream that resembles the visual noise seen on a television set tuned between channels. This stimulus contains motion signals of all speeds and directions at random. A coherent motion signal is added by displaying a fraction of the dots with a specific spatiotemporal relation to a randomly selected prior dot, that is, delayed a small amount in time and shifted a small amount in position. The fraction of coherently plotted dots we term the stimulus *correlation*. This stimulus is caricatured in Figure 1, which illustrates the spatiotemporal sequence for conditions of no, partial, and complete correlation. It is important to note that the display is dynamic; the lifetime of each dot is brief, preventing the subject from tracking identified moving features except when the correlation approaches 100%.

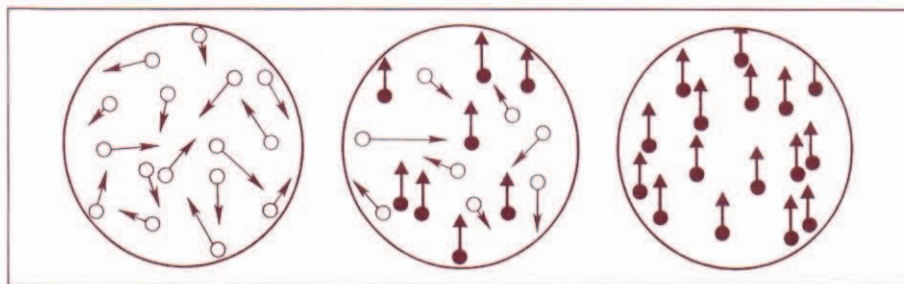
Under favorable conditions (with an interdot interval of about 50 ms and a spacing of about 0.1 deg, corresponding to a speed near 2 deg/s), human and monkey subjects can reliably report the direction of the motion of this coherent signal when the correlation exceeds 3% to 5%. Higher correlations are required for stimuli moving slower or faster than this optimal value.

We wished to explore the idea that psychophysical performance using this stimulus might depend on neurons like those found in area MT.

Two properties distinguish MT neurons from most neurons at lower levels of cortical processing. First, MT neurons are direction selective, responding well only to a narrow range of directions of motion; second, they can sum visual signals over rather large areas of the visual field. We were gratified to find in experiments with human observers that subjects could always identify the direction of motion of our stimuli when they could detect them at all. Moreover, their performance improved with increases in stimulus area up to at least 20 deg<sup>2</sup>, whereas other simple psychophysical tasks show asymptotic performance for areas of 1 deg<sup>2</sup> or less. Both findings are consistent with the idea that performance in this form of visual task is limited by signals carried by MT neurons.<sup>4</sup>

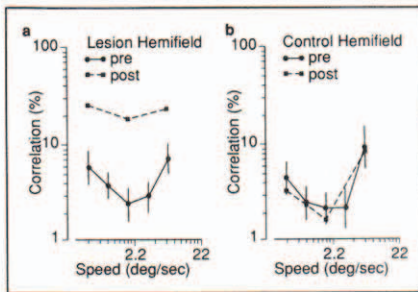
### MT SIGNALS ARE NECESSARY FOR MOTION DISCRIMINATION

To establish whether neurons in MT were necessary for monkeys to detect motion in this stimulus, we studied the effect of lesions of MT, using injections of the excitotoxin ibotenic acid to create small regions of damage without disrupting fibers of passage.<sup>5</sup> The results for a single monkey are shown in Figure 2. The solid curves show prelesion threshold correlation values for a range of



**Fig. 1.** A schematic illustration of the stimulus. The left panel shows purely random motion (0% correlation), the middle panel partially correlated motion (50%), and the right panel totally coherent motion (100%). From Newsome and Paré.<sup>5</sup>





**Fig. 2.** Effects of an MT lesion on psychophysical performance. (a) Elevation of direction discrimination thresholds in the hemifield contralateral to the lesion. The solid line shows the mean prelesion thresholds measured for five stimulus speeds; the error bars indicate the range of thresholds obtained. The dashed line shows thresholds obtained at three speeds on the day after an ibotenic acid injection into MT. (b) Lack of effect on direction discrimination thresholds in the ipsilateral hemifield. Conventions as in (a). From Newsome and Paré.<sup>5</sup>

stimulus speeds. Because MT on each side of the brain represents only the contralateral visual hemifield, measurements were made in the hemifield represented in the MT to be lesioned (Fig. 2a) and in the other hemifield (Fig. 2b). The dashed curves show the values measured on the first day after the lesion.

Direction discrimination thresholds in the lesion-affected hemifield rose by a factor of about 10, whereas those in the other hemifield were unchanged. Performance on a control contrast-detection task was unchanged after the lesion. It should be noted that this threshold elevation does not persist more than 3 to 5 days after small lesions, but larger lesions produce deficits from which recovery is incomplete. The mechanisms of recovery of function are not completely understood, but the fact that recovery can occur suggests that MT is not the *only* area through which visual motion signals can pass. The substantial transient elevation of threshold suggests, however, that signals carried by MT neurons are indeed necessary under normal circumstances for optimal performance on this task.

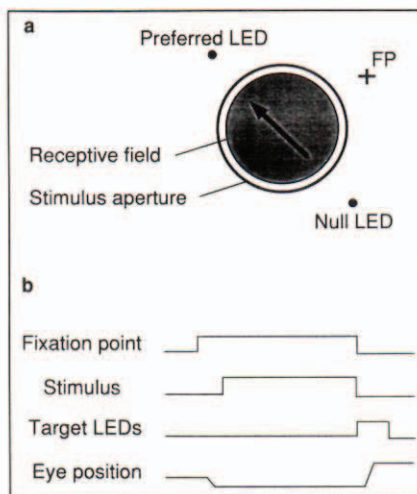
## MT SIGNALS ARE SUFFICIENT FOR MOTION DISCRIMINATION

The lesion experiments do not by themselves prove that the activity of MT neurons leads directly to the perception of motion. One might imagine that MT signals have some kind of permissive role, but do not themselves carry the visual motion information to higher centers. We therefore decided to record the activity of MT neurons while monkeys performed the visual motion task, with a view to learning whether the signals carried by the neurons contained the information necessary to support the observed perceptual judgment.<sup>6</sup>

The experimental procedure called for the monkey to discriminate between two possible directions of motion. Figure 3 schematically illustrates the experimental procedure. The monkey was trained to fixate on point FP, and the stimulus was presented within an aperture positioned over the *receptive field* of an MT cell (the region of the visual field within which stimuli had to be placed to excite the cell). The two

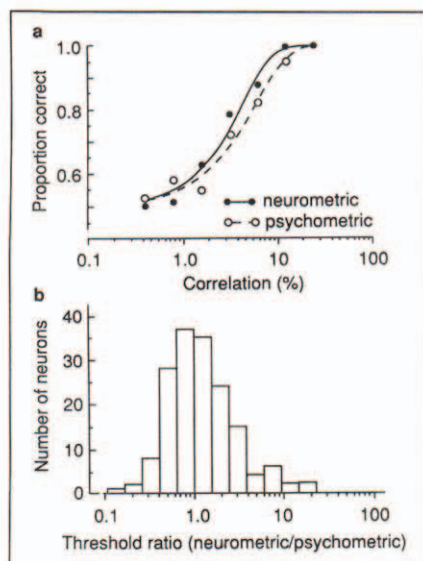
directions between which the monkey chose were set to correspond to the preferred (arrow) and null direction of movement for the neuron being recorded. At the end of the 2-s stimulus period, two LEDs appeared, each corresponding to one of the two possible directions of motion; the monkey signaled his judgment of direction by moving his eyes to one or the other LED. At the same time, we recorded and counted the impulses fired by the MT neuron, and compiled these counts into distributions of neuronal activity. The sequence of trials was randomized and included a range of correlation values for both directions of movement.

The responses of neurons in MT to any particular stimulus varied from trial to trial. At low correlations, the distribution of responses to stimuli that moved in the preferred direction overlapped the distribution of responses to null-direction stimuli. As the correlation increased, neurons became more vigorously active and more directionally selective, and the response distributions became more and more separated. We devised a statistical method to compute the performance of an MT neuron from these distributions and express that performance in terms of decision probabilities as a *neuro-metric* function of stimulus correlation.<sup>6</sup> The filled circles and solid curve in Figure 4a show such a function for a particular MT neuron. The open circles and dashed curve show the *psychometric* function describing the monkey's perceptual performance on the same set of trials on which the neuronal responses were measured. At low correlations, the monkey correctly chose the direction of stimulus motion on roughly half the trials, the proportion expected by chance alone. As correlation increased, performance improved to the perfect level, yielding a well-behaved psychometric function. Notice the close similarity of the two curves, and the fact that the



**Fig. 3.** A schematic illustration of the paradigm used in direction-discrimination experiments on awake monkeys. (a) The spatial arrangement of the display. (b) The temporal sequence of each trial. See text for details.





**Fig. 4.** Comparison of neuronal and psychophysical data obtained simultaneously from alert monkeys. (a) The filled circles and solid curve show a neurometric function relating theoretical neuronal choice probability to stimulus strength for a particular MT neuron. The open circles and dashed curve show the psychometric function describing the monkey's choice performance on the same set of trials on which neuronal measurements were made. The neurometric threshold (level at which 82% correct performance was achieved) for this neuron was 4.4%; the psychometric threshold was 6.1%. From Newsome Britten, and Movshon.<sup>6</sup> (b) Distribution of the ratio of neurometric to psychometric thresholds for 166 neurons recorded from two monkeys. Unpublished observations of W.T. Newsome, K.H. Britten, and J.A. Movshon.

thresholds (defined as the correlation supporting a level of 82% correct performance) for the two functions were very similar.

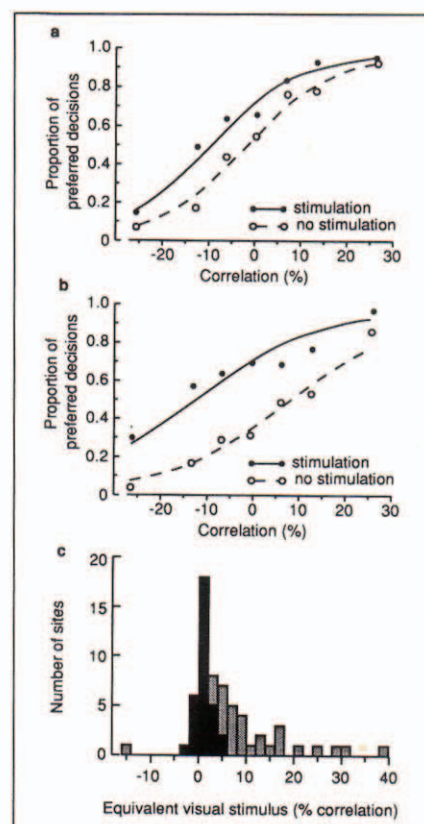
This similarity of thresholds was a general feature of our data. Figure 4b shows a distribution of the ratio of neuronal and psychophysical thresholds for 166 neurons from two monkeys. The modal value of the distribution was near 1, and for most cases, the psychometric and neurometric thresholds could not be distinguished statistically. This rather striking result suggests that the information used by the animal to make perceptual decisions might be carried by small numbers of MT neu-

rons, and it shows with certainty that the information needed for perceptual judgments is present in MT, and of sufficient quality to support the observed levels of performance.

### MODIFYING MT SIGNALS MODIFIES PERCEPTUAL JUDGMENTS OF MOTION

The results of the two previous experiments show that MT signals are necessary and sufficient for visual motion analysis. These findings suggest that it ought to be possible to affect performance by altering the activity of MT neurons, which we have done by delivering electrical microstimulation to small regions of MT.<sup>7</sup> Our notion was to enhance the representation of a particular direction of motion by selectively stimulating a group of MT neurons having similar preferred directions; this is possible because neurons within MT are grouped into columns of cells having similar directionality. We first recorded the direction preference of groups of MT neurons, then suitably positioned the microelectrode and delivered microstimulation through the electrode, using parameters intended to activate a spherical zone of tissue 150 to 200  $\mu\text{m}$  in diameter, containing roughly 100 neurons.

Microstimulation was delivered while the monkey made psychophysical judgments in a behavioral paradigm similar to that schematized in Figure 3. The major difference is that on half the trials, chosen at random, electrical stimulation was delivered for the 1-s period in which the visual stimulus was presented. Figures 5a and 5b show the outcomes of two experimental sessions involving two sites in MT. Each part of the figure plots the monkey's behavioral performance on trials in which no stimulation was delivered (open circles, dashed lines) and on trials in which stimulation was given



**Fig. 5.** The effect of electrical microstimulation of MT on direction-discrimination performance. (a) and (b) For two sites, the proportion of trials on which the stimulus was judged to move in the preferred direction is plotted against the strength of the motion signal. Positive correlations indicate motion in the preferred direction of recorded neurons; negative correlations indicate motion in the null direction. Open circles and dashed lines represent trials without electrical stimulation; filled circles and solid lines represent trials with electrical stimulation. The two curves in each plot are related to each other by a rigid horizontal shift equal to 7.7% correlation for the site in (a) and 20.1% correlation for the site in (b). From Salzman, Britten, and Newsome.<sup>7</sup> (c) Distribution of microstimulation effects obtained in 62 experiments in three monkeys. The effect of microstimulation in each case is given as the magnitude of the shift of the psychometric function produced by stimulation. Positive values indicate that the shift increased the probability that the monkey would choose the direction corresponding to the preference of the locally recorded neurons. Stippled columns indicate the 30 experiments in which a significant effect was observed ( $p < .05$ , logistic regression). From Salzman, Britten, and Newsome.<sup>7</sup>



(filled circles, solid lines). The correlation scale on the abscissa is altered to include both positive and negative values: Positive values represent stimuli moving in the direction preferred by the group of stimulated neurons, and negative values represent stimuli moving in the opposite direction. The ordinate plots the proportion of trials on which the monkey judged the stimulus to move in the preferred direction.

The effect of stimulation is evident in both cases. For each stimulus correlation, the monkey made more "preferred" decisions when electrical stimuli were present than when they were absent. The effect was modest for the stimulation site in Figure 5a and somewhat more robust for the site shown in Figure 5b. This effect can be captured by fitting the stimulation data with a leftward-shifted version of the curve used to fit the no-stimulation data; such pairs of curves are in fact plotted. The curves fit the data well, which means that the effect of the electrical stimulation can be considered equivalent to adding a particular proportion of real stimulus motion to the display; the horizontal distance between the curves can be taken as the *equivalent visual stimulus* added by the microstimulation.

Figure 5c plots the distribution of these equivalent visual stimuli for 62 stimulation sites in three monkeys. Positive shift values correspond to shifts of judgment to favor the preferred direction of the stimulated group of neurons (like the examples in Fig. 5a and b); stippled portions of the histogram represent cases in which the shift of the curves was statistically reliable. Stimulation produced reliable shifts in 30 cases; in 29 of these, the shift was in the preferred direction. Thus, when microstimulation has an effect on perceptual judgment, it is as if one

simply adds a constant visual motion signal to the intrinsic signals near the electrode tip. It is important to note that the effects of MT electrical stimulation will undoubtedly be felt elsewhere in the visual motion pathway, both through transsynaptic activation of other neurons and, possibly, through antidromic activation of neurons afferent to MT. But the effects of the stimulation are nonetheless closely tied to the properties of the local cluster of neurons being studied.

## CONCLUSION

The series of experiments described here explored the relationship between signals elicited in visual area MT by a suitably chosen visual stimulus and the resulting perceptual judgment of motion. We first verified the suitability of the stimulus by showing that in humans it seems—as intended—to be processed by motion-sensitive mechanisms. The lesion experiments show that it is necessary to have an intact area MT for optimal performance on motion judgments. The recording experiments show that signals carried by MT neurons are *sufficient* to support perceptual judgment. And the microstimulation experiments show that modification of MT signals *modifies* perceptual judgments in a manner consistent with the supposed role of these signals in supporting motion perception.

It is more difficult to assert that MT signals are the *only* ones available for perception. For one thing, MT is one station in an extended cortical pathway carrying signals about motion and other visual submodalities. For another, the ability of the system to recover—at least in part—from MT lesions suggests that

alternate pathways exist and can be used. Yet exploration of the extrastriate visual cortex yields the consistent impression that MT has a monothematic concern with motion, and that no other area so concentrates motion signals. MT is not a large area by the standards of the primate visual cortex, and it may be that its unique focus on motion arises because it is a bottleneck in the visual motion pathway through which the most informative signals must pass. Certainly such a focus is consistent with our deduction that MT does, indeed, carry the visual signals upon which the perception of motion is normally based.

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## Notes

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