



## Neural Mechanisms for Forming a Perceptual Decision

C. Daniel Salzman; William T. Newsome

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bands is taken into account, has been developed by Kasuya and his co-workers (36). This model is very successful in explaining the anomalous magnetic properties of CeSb and CeBi. A delicate balance between the crystal field splitting and the strength of the  $p$ - $f$  hybridization is responsible for the existence of the modulated phases with nonmagnetic planes in CeSb. Hydrostatic pressure destabilizes this delicate balance and leads to the disappearance of such phases.

### Related Areas

The complementary use of neutron and x-ray magnetic scattering techniques is extremely powerful for the study of magnetic materials. The experimental results for magnetic structures in rare earth metallic systems are established, and our theoretical understanding is quite reasonable, although not complete. Recently, a number of magnetic phases have been discovered in heavy fermion and high-temperature superconducting materials. These materials form a class of strongly correlated electron systems for which there is a possible interplay between magnetic interactions and superconductivity. These materials certainly merit a separate article.

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20. The periodicity of a magnetic structure is expressed in physical or direct space by the repeat distance (or the number of atomic layers) of the modulation wave. Physicists and crystallographers often use reciprocal, momentum, or wave-vector space. The physical realization of such a space is the space generated by the scattered beam. If  $a$ ,  $b$ , and  $c$  define the direct lattice, then their reciprocals  $a^*$ ,  $b^*$ , and  $c^*$  define the reciprocal lattice, which gives the positions of the nuclear Bragg peaks. The positions of the magnetic peaks of the antiferromagnetic structures or the positions of the satellite reflections of the modulated structures can be generated by the wave vector  $k$  from the reciprocal lattice vector  $H = ha^* + kb^* + lc^*$  ( $h$ ,  $k$ , and  $l$  are the Miller indices) by the relation  $G = H \pm k$ . For a simple antiferromagnetic structure, the wave vector components are simple fractions, namely,  $k = (1/2, 1/2, 1/2)$ . For a modulated structure, the components have in general nonrational values. For rare earth metals, the wave vectors of the modulated phases are given by  $k = (0, 0, k_z)$ , where  $k_z$  is expressed in units of  $c^*$ .
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## RESEARCH ARTICLE

# Neural Mechanisms for Forming a Perceptual Decision

C. Daniel Salzman and William T. Newsome\*

Cognitive and behavioral responses to environmental stimuli depend on an evaluation of sensory signals within the cerebral cortex. The mechanism by which this occurs in a specific visual task was investigated with a combination of physiological and psychophysical techniques. Rhesus monkeys discriminated among eight possible directions of motion while directional signals were manipulated in visual area MT. One directional signal was generated by a visual stimulus and a second signal was introduced by electrically stimulating neurons that encoded a specific direction of motion. The decisions made by the monkeys in response to the two signals allowed a distinction to be made between two possible mechanisms for interpreting directional signals in MT. The monkeys tended to cast decisions in favor of one or the other signal, indicating that the signals exerted independent effects on performance and that an interactive mechanism such as vector averaging of the two signals was not operative. Thus, the data suggest a mechanism in which monkeys chose the direction encoded by the largest signal in the representation of motion direction, a "winner-take-all" decision process.

Within the cerebral cortex, the visual environment is encoded by the electrical activity of neurons in topographically organized maps of visual space. Little is known, however, about how the neuronal signals within a sensory representation are inter-

preted to form perceptual decisions that guide behavior. Such decision processes have been extensively modeled in cognitive psychology and psychophysics to provide quantitative accounts of human performance in a variety of discrimination tasks (1). Physiological approaches that test and refine such models are essential for understanding the neural basis of cognitive behavior. Here we describe a physiological experiment that explores how sensory sig-

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nals are evaluated to judge the direction of moving visual stimuli in a specific psychophysical task.

In monkeys, neural signals related to the perception of motion are carried within a specialized pathway in visual cortex (2). Neurons in this motion pathway are predominantly direction-selective; they respond maximally to visual stimuli moving in a preferred direction but little or not at all to motion in the opposite direction. Within the motion pathway, the middle temporal area of dorsal extrastriate cortex (MT, or V5) contains a systematic representation of motion direction (3). Almost all MT neurons are direction-selective, and these neurons are organized in a columnar fashion so that neighboring neurons tend to have a similar preferred direction and receptive field location. Each cortical column therefore encodes a particular direction of motion in a restricted region of the visual field. Cortical columns may differ in receptive field location and preferred direction, thus forming a topographic representation of all directions of motion (4).

In a direction discrimination task, at least two competing hypotheses—vector averaging and winner-take-all—could explain how activity within this system of columns is evaluated in order to form a perceptual decision. In a vector averaging model, the responses of neurons encoding all directions of motion are weighted and pooled to obtain an accurate estimate of motion direction. In this model, each neuron “votes” for its preferred direction with a weight proportional to its response intensity. The average of all individual neuronal vectors yields a population vector, indicating the direction of stimulus motion that elicited the observed pattern of activity in MT (5, 6). This proposal is similar to motor mechanisms that control the metrics of saccadic eye movements (7) and also, perhaps, of reaching arm movements (8).

Although a vector averaging model may be correct for some moving stimuli, it cannot account for perceptual phenomena like motion transparency in which two directions of motion are perceived simultaneously when two moving dot patterns are spatially superimposed (9). Motion transparency indicates that directional signals need not be averaged together, but can be kept segregated in the neural representation of motion.

The segregation of signals is a central feature of a winner-take-all model, in which the direction of stimulus motion is identified by monitoring several direction-specific channels. Decisions are cast in favor of the channel generating the largest signal. In the present context, a channel may be considered to be one or a few columns in MT that encode a particular

motion direction (10). Winner-take-all models account nicely for perceptual data acquired in several common psychophysical procedures (1), and they can also be applied to physiological data to predict accurately psychophysical performance (11, 12).

To distinguish between vector averaging and winner-take-all mechanisms in a specific perceptual task, we applied electrical microstimulation to directional columns in MT, while rhesus monkeys performed an eight-alternative direction discrimination (13–15). Evidence for vector averaging could emerge when the direction of visual stimulus motion differed by 90 or 135 degrees from the preferred direction of the stimulated neurons. Under these conditions, a vector averaging model predicts that the monkeys’ choices will be biased toward directions of motion intermediate between the two directional signals. In contrast, a winner-take-all model predicts that the two directional signals will compete with each other, with choices being made in favor of the channel of neurons responding most strongly. In this case, microstimulation and the visual stimulus exert independent effects on the monkeys’ choices. Decisions will tend to be cast in favor of one of the two directional signals if these directions are separated sufficiently. Our data support the winner-take-all mechanism; the monkeys’ performance could be accounted for by independent contributions from microstimulation and the visual stimulus. We observed no interactions between microstimulation and the visual stimulus that could support a vector averaging mechanism.

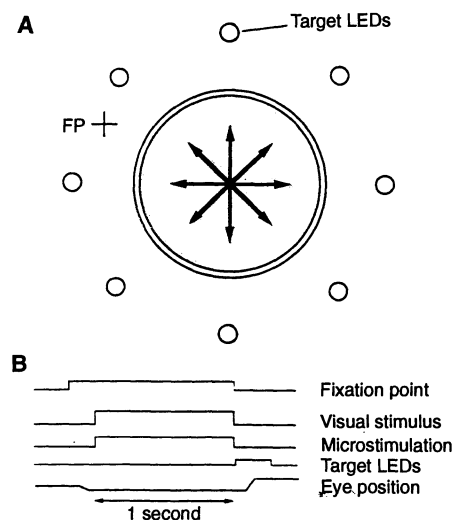
**Stimulation sites and the behavioral task.** For each experiment, we positioned a microelectrode within a cortical column encoding a particular direction of motion (16–18). The multiunit receptive field was mapped with a bar of light, and we then presented visual stimuli consisting of dynamic random dot patterns within an aperture placed directly over the neurons’ receptive field (11). The strength of a motion signal within the random dot display was determined by the percentage of dots carrying a unidirectional motion signal. We refer to this percentage as the correlation of the motion signal, and the correlation could vary from 0 to 100 percent. The remaining uncorrelated dots were displaced randomly in the display, creating a masking motion noise. Thus the difficulty of the eight-alternative discrimination could be adjusted simply by presenting a different correlation of the motion signal.

Before starting a microstimulation experiment, we used a dot pattern with 100 percent correlation to measure the directional tuning properties of neurons at the stimulation site. Multiunit responses were measured for each of eight directions of

motion separated by 45 degrees while monkeys performed a fixation task (19).

During a discrimination experiment, a monkey fixated a point of light (Fig. 1A, FP) while viewing the dynamic random dot stimulus presented within the visual stimulus aperture placed over the neurons’ receptive field. For an individual trial, the direction of motion in the visual stimulus was one of the eight possible directions (Fig. 1A, arrows). The direction was selected randomly on each trial, and the speed of the correlated motion signal was the optimal speed of the neurons under study. At the end of a 1-s viewing interval, the visual stimulus and fixation point were extinguished, and eight light-emitting diodes (LEDs) were turned on, one corresponding to each possible direction of motion. The monkey indicated its judgment of motion direction by making a saccadic eye movement to one of the LEDs. Correct choices were rewarded with drops of water or juice. We trained two monkeys on this task until their performance under a wide range of stimulus conditions no longer improved. The monkeys usually performed almost perfectly (>90 percent correct) when the correlation was high (>50 percent correlated dots). At low correlation values (below 10 percent correlated dots, for example), performance approached chance values.

While a monkey performed the eight-alternative discrimination, we attempted to



**Fig. 1.** (A) The experimental set-up for the eight-alternative direction discrimination. The monkey fixated a light-emitting diode (LED) labeled FP and viewed the visual stimulus presented within an aperture (outer circle) placed directly over the receptive field of neurons at the stimulation site (inner circle). Motion in the stimulus could occur in any of eight directions (arrows) over a range of correlation levels. (B) The timing of events within a trial containing microstimulation. Microstimulation was applied simultaneously with the presentation of the visual stimulus.

introduce a directionally specific signal into the cortex by activating neurons at the stimulation site with trains of small-amplitude stimulating pulses (10  $\mu$ A, biphasic pulses) (20). Microstimulation was applied for 1 s, beginning and ending simultaneously with the onset and offset of the visual stimulus (Fig. 1B). In a typical experiment, the monkey discriminated the direction of motion at six or seven correlation values spanning 0 to 100 percent correlation. Microstimulation usually occurred on half of the trials at all but the two highest correlation values; the values excluded from the microstimulation regime helped ensure that the monkey's reward rate was sufficiently high to maintain motivated performance. For both the stimulated and nonstimulated conditions, an equal number of trials (usually five) was presented in each direction for each correlation value. At 0 percent correlation, where the stimulus cannot cue a correct choice, we rewarded the monkey randomly. Reward contingencies were identical for stimulated and nonstimulated trials, and all trial types were randomly interleaved.

**Performance on the eight-alternative discrimination.** Microstimulation frequently had a striking effect on the monkeys' decisions (for example, Fig. 2). Data from

this experiment have been collapsed across the eight visual stimulus directions to indicate the overall proportion of decisions made in each direction. The monkey's choices were influenced by at least three factors: (i) an inherent "choice bias," (ii) microstimulation, and (iii) the visual stimulus. The monkey's inherent choice bias can be observed in the nonstimulated condition at very low correlation values, where the visual stimulus supplies little or no directional information. Under these conditions, the monkey chose the rightward direction more frequently than would be expected by chance (>12.5 percent of the decisions) (Fig. 2, A and B), revealing an inherent choice bias toward the right. The choice bias could be overcome either by microstimulation or by the presence of a strong motion stimulus. The effect of microstimulation on the choices is demonstrated by the large increase in decisions made down and to the left on stimulated trials (Fig. 2, A through D). The effect of the visual stimulus, while large, is not directly obvious in these polar plots because the data have been collapsed across visual stimulus direction. However, the monkey made approximately equal numbers of choices in each direction at high correlation values (51.2 percent and 100 percent)

(Fig. 2, E and F), reflecting nearly perfect performance when the visual stimulus contained a strong motion signal. (Equal numbers of trials were presented in each direction for each correlation value.)

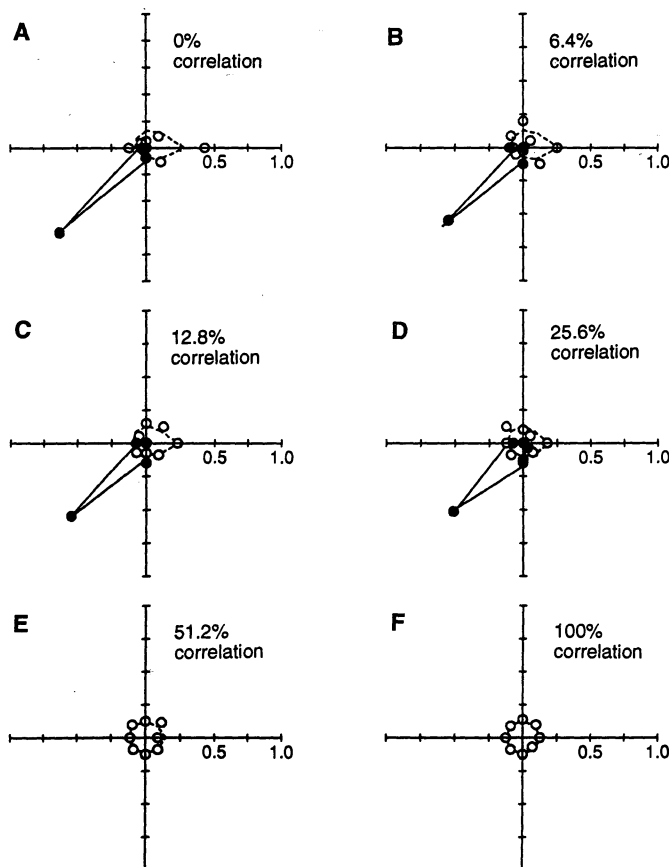
Analysis of these data had to accommodate the large number of test conditions within an experiment (usually 528 combinations of stimulus and response options). We developed a statistical model, based on polychotomous logistic regression, that predicted performance from three types of parameters, corresponding to the three influences evident in Fig. 2—choice bias, microstimulation, and the visual stimulus (21).

In its simplest form, the statistical model assumed independent contributions from each free parameter. Eight parameters described choice bias, one for each choice direction. If the data from an experiment revealed no choice bias, the eight bias coefficients were equal. An additional eight parameters described the effect of microstimulation, one corresponding to each of the eight possible directions. Finally, five parameters described the relation between the direction and strength of motion in the visual stimulus and a monkey's decisions. The first of these five parameters modeled the influence of the visual stimulus on decisions made to the same direction as the visual stimulus. The remaining four parameters modeled the effect of the visual stimulus on decisions made to directions  $\pm 45^\circ$ ,  $\pm 90^\circ$ ,  $\pm 135^\circ$ , and  $\pm 180^\circ$  degrees away from the direction of stimulus motion. Because the monkeys accurately reported the direction of motion in the stimulus at high correlation values, the fitting of the model to the data always estimated the first stimulus parameter to have the largest value, with the values of the other parameters tending to decrease as the angle between stimulus and choice directions increased. The use of these five parameters to model the contribution of the visual stimulus to performance required two assumptions: (i) the monkey's sensitivity to the visual stimulus on average does not vary with the direction of the motion signal, and (ii) given motion in a particular direction, the monkey's decisions are symmetrically distributed about that direction in the absence of bias.

We used a maximum likelihood fitting method to provide quantitative estimates and measures of statistical significance for each parameter (22). Our criterion for statistical significance of a parameter in the model was  $P < 0.01$ . The model provided an excellent description of the data for every experiment (23), with model predictions closely matching observed data (for example, Fig. 2, dashed and solid lines).

**Interaction between microstimulation and the visual stimulus.** To distinguish

**Fig. 2.** Polar plots showing monkey performance (circles) and model predictions (lines) for an eight-alternative microstimulation experiment. The preferred direction of neurons at this stimulation site was down and to the left. The data have been collapsed across visual stimulus direction so that one polar plot describes all choices made at a particular correlation. Open circles, performance on nonstimulated trials; closed symbols, the data from stimulated trials. Dashed lines, model predictions for nonstimulated data; solid lines, predictions for stimulated data. Data predicted by the model are at the vertices of each of the line plots; the vertices are connected with lines only for the purpose of presentation. Microstimulation was not applied at 51.2 percent and 100 percent correlation, and therefore only data and predictions for the nonstimulated condition appear. Eighty trials were performed at each correlation value.



between vector averaging and winner-take-all mechanisms for forming decisions about motion direction, we examined conditions where the visual stimulus and microstimulation both influenced decisions. We could not detect vector averaging if either the visual stimulus or the microstimulation effect was sufficiently strong to overwhelm the other signal. We therefore analyzed a subset of data chosen to maximize our chances of detecting interaction effects; in this subset both microstimulation and the visual stimulus had a statistically significant impact on performance (24).

The selected subset of data comprised 27 stimulus correlation values from 23 experiments. For each selected condition, we extracted the data when the direction of visual stimulus motion was 90 or 135 degrees away from the preferred direction of the microstimulation effect and analyzed the pattern of decisions made under these conditions (25) (Fig. 3, A and B). Each of the 27 selected conditions actually contributed two sets of data in this analysis, as stimulus motion was presented both clockwise and counterclockwise from the microstimulation effect direction.

When the direction of stimulus motion and microstimulation effect differed by 135 degrees, the monkeys made the most decisions in favor of the visual stimulus direction, with somewhat fewer decisions made to the microstimulation effect direction (Fig. 3A, open symbols). As expected from a winner-take-all mechanism, fewer decisions were made in favor of directions intermediate between the two directional signals. The model predictions closely matched the observed data (Fig. 3A, solid symbols). Recall that the model estimates the effects on decisions of microstimulation, the visual stimulus, and choice bias under the assumption that these factors contribute independently to decisions. The model cannot incorporate specific interactions such as vector averaging between different directional signals (26). Since independent contributions of microstimulation and the visual stimulus account for psychophysical performance, our data support a winner-take-all decision mechanism.

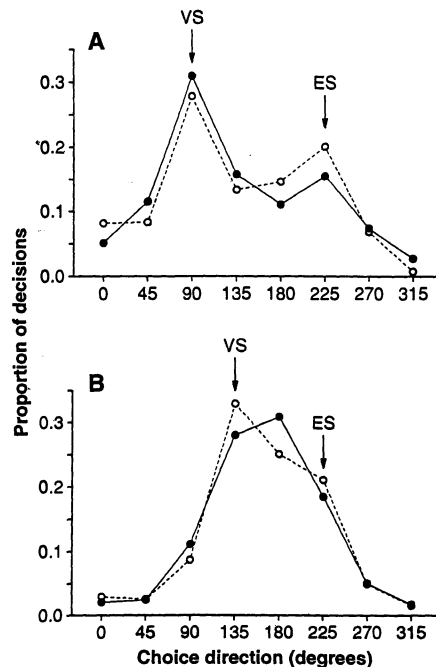
When the visual stimulus and microstimulation effect directions differed by 90 degrees, the monkeys made slightly more decisions to the direction intermediate between the two-directional signals than one might intuitively expect (Fig. 3B, open symbols). A winner-take-all mechanism, however, would predict an increase in choices to intermediate directions when the two directional signals are broadly tuned and not substantially separated (27). In fact, the statistical model, which does not incorporate vector averaging, predicts a higher proportion of decisions in favor of

the intermediate direction than was observed in the data (Fig. 3B, solid symbols). Thus the monkeys made even fewer choices to the intermediate direction than would be expected if microstimulation and the visual stimulus contributed independently to decisions. This might occur if the subpopulation of neurons encoding the intermediate direction was inhibited by the visual stimulus and microstimulation (28).

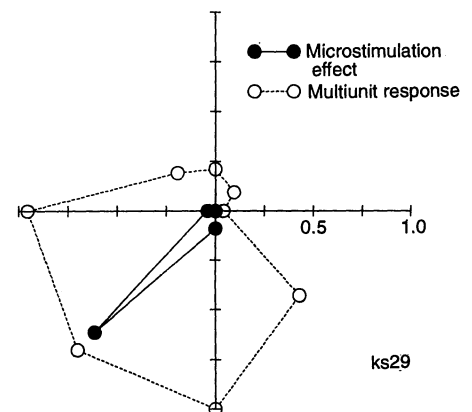
To confirm that the averaged data in Fig. 3 did not disguise vector averaging effects in individual experiments, we explicitly tested the interaction hypothesis on an experiment-by-experiment basis. For each of the 27 selected conditions, we fit the experiment containing the selected condition with an expanded version of the model containing two interaction terms (29). One of the new terms estimated interaction effects when the direction of visual stimulus motion was orthogonal to the preferred direction of the microstimulation effect. The second new term assessed interaction when the visual stimulus moved in a direction 135 degrees from the pre-

ferred direction of the microstimulation effect. The interaction terms only modeled choices made when the visual stimulus was at the correlation value specified by the screening tests described above. The new terms allowed the model to capture nonlinear interactions between the visual stimulus and the microstimulation signal that would not be fit under the assumption of independence of the two signals. Positive interaction terms would reflect increased choices relative to the original model toward directions intermediate between the visual and microstimulation signals. This result would be consistent with the vector averaging model.

In 52 of the 54 conditions tested (96 percent), the interaction term was not significantly different from zero. Of the two significant interaction terms, one was positive and the other was negative. In addition, the mean of the interaction terms was not significantly different from zero for the 27 conditions where the direction of stimulus motion differed from the direction of the microstimulation effect by 135 degrees. The mean of the interaction terms was significantly less than zero when visual stimulus motion was orthogonal to the direction of the microstimulation effect. Negative interaction terms imply that fewer decisions were made to the intermediate direction than expected on the assumption of independence. This result is consistent with the averaged data in Fig. 3B, which show that fewer decisions were made in favor of the intermediate direction (180 degrees) than predicted by the original model.



**Fig. 3.** The pattern of decisions made when the visual stimulus (VS) differed by (A) 135 or (B) 90 degrees from the preferred direction of the microstimulation effect (ES). Open symbols, the average proportion of the decisions made in each of eight response directions; closed symbols, model predictions for the same data. Before averaging the selected data, each data set was rotated so that the preferred direction of the microstimulation effect corresponded to 225 degrees. The data were also symmetrically folded over so that visual stimulus motion clockwise to the microstimulation effect direction could be represented on the same plots as motion counterclockwise.



**Fig. 4.** The behavioral effect of microstimulation compared to the directional tuning of neurons at the stimulation site (experiment from Fig. 2). To describe the microstimulation effect (filled circles and solid lines), for each response direction the predicted probabilities were plotted under the assumption that the only factor affecting the monkey's choices was microstimulation. In the plot of neuronal response as a function of visual stimulus direction, the maximum response was normalized to equal 1.0 (open circles and dashed lines). Monkey ks29.

Our data therefore provide no evidence for vector averaging between the visual and microstimulation signals. Considering the data set as a whole, the pattern of choices made by the monkeys is well described by modeling the visual stimulus and microstimulation signal as independent influences on performance.

**Characterization of the microstimulation effects.** MT is thus far unusual in that psychophysical performance can be manipulated predictably by activating functionally defined cortical circuits with microstimulation. Because microstimulation exerts an independent influence on performance, the model enabled us to compute the directional properties of each microstimulation effect without the confounding influences of choice bias and the visual stimulus. To accomplish this, we calculated for each experiment the probability of decisions occurring in each of the eight possible directions assuming microstimulation was the only factor affecting the monkeys' choices. The bias and visual stimulus coefficients in the model were set equal to zero. For the experiment in Fig. 2, the computed microstimulation effect was specific for the preferred direction of neurons at the stimulation site, and the directional tuning of the behavioral effect was substantially narrower than that of the neurons (30) (Fig. 4).

To compare quantitatively the microstimulation tuning curve to the visual tuning curve of neurons at the stimulation site, we fit separate Gaussian functions to the two sets of data (31). The fit Gaussian functions produced a mean and standard deviation ( $\sigma$ ) for both the neuronal and

microstimulation data, allowing us to compare directly the preferred directions and bandwidths of the microstimulation and visual response data. For the experiment in Fig. 4, the preferred directions differed by only 6 degrees, but the bandwidth of the visual tuning curve was 43 degrees wider than that of the microstimulation tuning curve ( $\sigma = 70.8$  degrees for visual responses;  $\sigma = 27.5$  degrees for microstimulation).

We performed this analysis for each of the 44 experiments (out of 66 total) in which microstimulation had a significant effect on the monkey's choices. Since the visual responses of MT neurons are broadly tuned, the preferred direction of the microstimulation effect generally fell within the excitatory bandwidth of the visual tuning curve (Fig. 5). In fact, 80 percent of the behavioral effects (35 out of 44) had a preferred direction within 45 degrees of the preferred direction of neurons at the stimulation site. The absolute value of the difference in preferred direction was inversely correlated with the size of effects ( $r = -0.46$ ;  $P < 0.01$ ) (32), indicating that the alignment of the preferred directions was more precise when a large effect occurred.

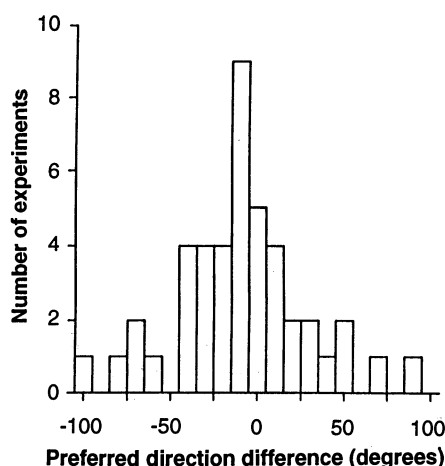
As in the experiment in Fig. 4, the microstimulation tuning curves tended to be narrower than the visual tuning curves of neurons at the stimulation site. When the microstimulation tuning bandwidth was plotted as a function of visual tuning bandwidth (Fig. 6), the bandwidth of the behavioral effect was usually narrower than that of the visual responses (data points below the diagonal). The mean difference in bandwidth was 18 degrees, indicating a 29 percent decrease in behavioral bandwidth relative to visual tuning bandwidth (paired

$t$  test;  $P \leq 0.0001$ ) (33). The narrow tuning of microstimulation effects was even more striking for experiments showing large effects, as the size of the effect was inversely correlated with behavioral bandwidth ( $r = -0.49$ ;  $P < 0.001$ ). For the 22 experiments with the largest effects, the difference in bandwidth was 27 degrees, corresponding to a 44 percent decrease in behavioral relative to neuronal bandwidth. Experiments with large effects therefore tended to produce narrow tuning curves well aligned with the preferred direction of neurons at a stimulation site. These conditions probably arise when the stimulating electrode is particularly well positioned, perhaps in the middle of a cortical column.

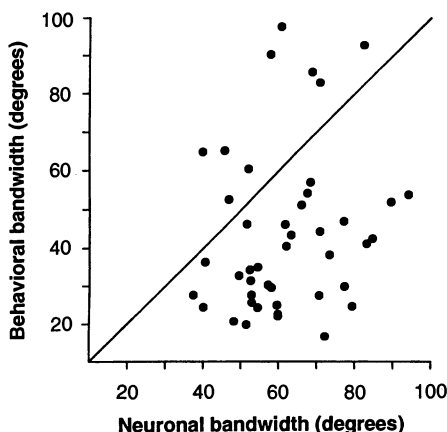
**Neural mechanisms for forming a perceptual decision.** Our results provide physiological evidence that distinguishes between two mechanisms for forming a perceptual decision on an eight-alternative direction discrimination. We found that the directional signals elicited by microstimulation and the visual stimulus exerted independent effects on performance. These effects may be explained if monkeys used a winner-take-all mechanism to form decisions on the task. In this mechanism, a comparison of activity in distinct subpopulations of neurons, each encoding a particular direction of motion, results in a decision favoring the largest signal. The independent effects of microstimulation and the visual stimulus arise directly from their differential influence on specific subpopulations of direction selective neurons.

Our data do not rule out the possibility that vector averaging of neuronal signals occurs within each subpopulation of neurons. In fact, the narrow tuning of microstimulation effects, as compared to the tuning of MT neurons, could result from a local vector computation. We found no evidence, however, that decisions on this task rely on a vector computation across neurons encoding all directions of motion. Our results therefore show that directional signals can be segregated and evaluated independently to support performance on tasks like our eight-alternative direction discrimination. The segregation of directional signals, however, does not imply that microstimulation caused a subjective impression similar to motion transparency in our experiments. The perception of a second transparent dot field would almost certainly require intricate patterns of activity in V1 and other extrastriate areas that microstimulation in MT cannot replicate.

Although our data clearly demonstrate the existence of a winner-take-all decision process for the eight-alternative direction discrimination, both vector averaging and winner-take-all mechanisms probably operate in the visual system, depending upon



**Fig. 5.** The difference between the preferred direction of microstimulation effect and that of the neurons recorded at the stimulation site in each experiment in which microstimulation had a significant effect. This difference is defined as the preferred direction of the neurons minus the preferred direction of the behavioral effect, as characterized by the Gaussian fits to neuronal and behavioral data.



**Fig. 6.** The bandwidth of the behavioral effect of microstimulation from every experiment with a statistically significant effect plotted as a function of the directional bandwidth of the neurons recorded at the corresponding stimulation site. Bandwidth is defined as  $\sigma$ , which was derived from Gaussian fits to behavioral data and to neuronal data, respectively.



the nature of the visual stimuli and the demands of the task being performed. For example, a stimulus in which dots move randomly within a restricted range of directions results in a unidirectional motion percept, suggesting that a vector averaging mechanism underlies perception of this stimulus (34). More complicated mechanisms than either vector averaging or winner-take-all must also exist. For example, the psychophysical phenomenon of motion coherence, in which a single direction of motion is perceived when two sine wave gratings moving in different directions are spatially superimposed, suggests a sophisticated "intersection of constraints" mechanism (35). It is interesting that some neurons in MT respond to the superimposed gratings as predicted by this mechanism (36). Thus neural signals for visual motion are probably combined in multiple ways to form decisions in different perceptual tasks with greatly varying demands.

Sensory systems represent diverse stimuli present simultaneously in the environment. Motor control, by contrast, is inherently more serial because movements of any body part are executed one at a time. Thus motor systems may rely more on broadly based averaging mechanisms (7, 8, 37, 38), having no need to code different movements simultaneously. From this point of view, a critical problem in sensorimotor integration is the selection of single targets for movement from a large array of environmental stimuli. The decision mechanisms that accomplish this selection are becoming an increasingly important subject of investigation for cognitive neuroscience.

## REFERENCES AND NOTES

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- For the purposes of this article, we do not distinguish between vector averaging models and vector summation models. It is not clear that the two models would produce distinct predictions concerning the perception of motion of a visual stimulus.
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- The precision with which a winner-take-all model may estimate motion direction is limited by the number of monitored channels and the "distance" between channels.
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- Enhancing the activity of neurons encoding a particular direction of motion biases monkeys' choices on a two-alternative task in which monkeys discriminate between two opposite directions of motion (14, 15). These results may be explained by either vector averaging or winner-take-all models. In a winner-take-all model, choices would be made by monitoring two channels, with the decision being cast in favor of the channel offering the strongest signal. On the other hand, a decision mechanism based on vector averaging would first compute the vector average of all directional signals available. This would produce a population vector pointing to a particular direction of motion. A decision rule would then be applied to the population vector to generate an actual choice on the two-alternative discrimination. Assuming a decision rule that chooses the direction closest to the population vector, the two models can produce similar predictions.
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- Our techniques for physiological recording and behavioral control have been described (14). Eye movements were monitored with the scleral search coil technique (17). During recording sessions a monkey sat in a primate chair facing a cathode ray tube (CRT) monitor 57 cm away, upon which we presented visual stimuli. For each experiment, the monkey's head was held stationary by connecting a surgically installed head implant to the primate chair. A recording cylinder located over the occipital lobe permitted electrode access to visual cortex. Electrodes were inserted into MT through a transdural guide tube (18). Monkeys were required to fixate a point of light while we searched for a stimulation site. Our formal criterion for positioning the electrode was that neurons had to have similar physiological properties for at least 150  $\mu$ m of electrode travel. We then positioned our electrode in the middle of such a cluster.
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- Multiunit responses were measured with a window discriminator. The lower boundary of the window was set at approximately half the amplitude of the maximum signal observed.
- We used the same microstimulation parameters as in previous experiments involving two-choice discrimination discriminations (14, 15): 10- $\mu$ A biphasic pulses, each with a duration of 200  $\mu$ s, with a 100- $\mu$ s interval between the cathodal leading pulse and the anodal pulse. See (14) for a discussion of issues concerning neuronal activation with microstimulation. For all experiments, we used tungsten microelectrodes (Microprobe, Inc.) with 20 to 30  $\mu$ m of exposed tip (resistance usually <1.0 Mohm at 1 kHz). We typically plated the tip of an electrode with gold before an experiment, substantially reducing the electrode's resistance.
- For a brief discussion of polychotomous logistic regression see D. R. Cox and E. J. Snell [*Analysis of Binary Data* (Methuen, London, 1989)]. In the specific model that we used, the probability of a decision in the  $i$ th direction,  $P_i$ , is a function of the visual stimulus presented and microstimulation
 
$$P_i = \frac{\exp(y_i)}{\sum_{j=1}^8 \exp(y_j)} \quad \{i = 1 \dots 8\} \quad (1)$$
 where
 
$$y_j = \alpha_j + \beta_j z_1 + \gamma_d x \quad (2)$$
 In these equations,  $\alpha_j$  represents the contribution of choice bias for the  $j$ th response direction, and  $\beta_j$  models the effects of microstimulation for the same direction.  $\beta_j$  is multiplied by  $z_1$ , which equals 1 when microstimulation is applied, but 0 when there is no microstimulation. The visual stimulus parameters are represented notationally by  $\gamma_{1-5}$ . These terms are specified in Eq. 2 by  $\gamma_d$ , where  $d$  indicates a particular visual stimulus parameter according to the difference in angle between a response direction,  $j$ , and the direction of the visual stimulus.  $\gamma_1$  is used when stimulus direction and response direction are identical (that is, when stimulus motion is in the  $j$ th direction). Similarly, when motion is 45 degrees from the  $j$ th direction,  $\gamma_2$  is included. For motion 90, 135, and 180 degrees away from the  $j$ th direction,  $\gamma_3$ ,  $\gamma_4$ , and  $\gamma_5$ , respectively, are used. In each instance, the designated  $\gamma$  parameter is multiplied by  $x$ , the correlation of the visual stimulus. This system of equations estimates the proportion of choices in eight directions for each combination of visual and electrical stimulation. We used maximum likelihood methods to find the best fitting parameters  $\alpha_{1-8}$ ,  $\beta_{1-8}$ , and  $\gamma_{1-5}$ .
- To permit quantitative estimation of the parameters in the model, we arbitrarily set three parameters ( $\alpha_8$ ,  $\beta_8$ , and  $\gamma_5$ ) equal to 0. The other parameters are therefore estimated relative to the three preset parameters. Presetting these parameters in this manner did not affect the predictions of the model nor the identification of experiments containing significant microstimulation effects.
- To assess the fit of the model to data from each experiment, we performed a goodness-of-fit test based on log-likelihood ratios. This test failed to reject the fit from any experiment ( $P > 0.5$  in all cases).
- For each experiment in which microstimulation had a significant effect (at least one significant  $\beta$  term), we screened correlation values by performing two chi-square tests of association. The first analysis tested the null hypothesis that the direction of the monkeys' choices on stimulated trials was unrelated to the direction of the visual stimulus. The second analysis tested the null hypothesis that the direction of choices was unrelated to the presence or absence of microstimulation. A correlation value was included in the interaction analysis only if both tests revealed a significant association ( $P < 0.05$ ).
- The preferred direction of the microstimulation effect was determined by the fit of the model described by Eqs. 1 and 2. We defined this direction according to which stimulation coefficient  $\beta_j$  was greatest.
- To confirm that the model could not account for interactions such as vector averaging, we performed an analysis of residual errors. One might think that vector averaging could be incorporated into the model by increasing the estimate of microstimulation parameters corresponding to di-

rections 45 or 90 degrees from the microstimulation effect direction. Choices to these directions would be affected by a vector averaging mechanism when visual stimulus motion is 90 or 135 degrees away from the microstimulation effect direction. The change in parameter estimates would thereby permit accurate description of the effects of vector averaging. But predicted choices in this case would be affected independent of visual stimulus direction, because the increased estimates of microstimulation parameters would influence predictions regardless of visual stimulus direction. This would lead to systematic errors in the predicted choices for those conditions in which vector averaging is irrelevant (for example, when the visual stimulus was in the same direction as the microstimulation effect or in a direction 45 degrees away). Examination of data and predictions for the 27 selected correlation values revealed no evidence of systematic error under such conditions (the mean value of each set of residual errors was not significantly different from 0; *t* test,  $P > 0.1$ ). This analysis confirmed that an interaction such as vector averaging between signals generated by microstimulation and the visual stimulus cannot be described with this version of the model. To account for a vector averaging effect, the model must include terms allowing a specific interaction between the visual stimulus and microstimulation.

27. A winner-take-all mechanism is based on a comparison of the sum of activity in distinct subpopulations of neurons encoding different motion directions. If two broadly tuned directional responses, differing in preferred direction by 90 degrees, are introduced into cortex, then the peak of activity across the entire population of neurons may correspond to the direction intermediate between the two preferred directions. In this case, a winner-take-all mechanism will decide in favor of this intermediate direction.
28. Consistent with this finding, psychophysical experiments have shown that the perceived angle between two patterns of spatially superimposed random dots is overestimated for angle differences of up to 90 degrees, also suggesting a mechanism that relies on inhibition (12). In addition, a model of the perception of motion in plaid grating patterns incorporates inhibition between adjacent direction channels [H. R. Wilson, V. P. Ferrera, C. Yo, *Visual Neurosci.* 9, 79 (1992)].
29. To implement the interaction analysis, the model

described by Eqs. 1 and 2 was first fit to determine the preferred direction of the microstimulation effect; we defined this direction according to which stimulation coefficient  $\beta_j$  was greatest. The interaction terms were then added to the model in an appropriate manner given the direction of the microstimulation effect. The model including interaction terms is still described by Eq. 1, but the equation for  $y_j$  (Eq. 2) was modified to

$$y_j = \alpha_j + \beta_j z_1 \gamma_{\sigma} x + \delta_1 z_2 + \delta_2 z_3 \quad (3)$$

Here  $\delta_1$  is the interaction coefficient when the two directional signals differ by 90 degrees, and  $\delta_2$  is the term for a difference of 135 degrees.  $z_2$  and  $z_3$  are dummy variables that allow  $\delta_1$  and  $\delta_2$  to affect model predictions only when conditions are appropriate for vector averaging. Specifically,  $z_2$  assumes a value of unity when the response direction ( $j$ ) is intermediate between two orthogonal directional signals. Otherwise,  $z_2$  is zero. Similarly,  $z_3$  is unity only when  $j$  is intermediate between directional signals separated by 135 degrees. For the four experiments that contained two correlation values appropriate for analysis, we performed separate fits of the model to test interaction at each correlation value independently. Note that the interaction terms assumed symmetry; the value of the coefficient was the same regardless of whether the visual stimulus was clockwise or counterclockwise to the preferred direction of the microstimulation effect.

30. In the experiment in Fig. 4, the effect of microstimulation was sufficiently strong that the modeled microstimulation effect was very similar to the plot of actual performance on stimulated trials at 0 percent correlation (compare with Fig. 2A). For experiments with smaller effects, however, microstimulation did not completely overcome the effects of choice bias, as the monkey made choices on stimulated trials both toward the bias direction and toward the direction of the microstimulation effect. In those cases, the model provides an accurate description of the microstimulation effect independent of choice bias.
31. We fit the data with a Gaussian function that had four free parameters: a baseline parameter allowing the tails of the function to asymptote at non-zero values, a parameter characterizing the center of the distribution, a parameter that quantified the bandwidth of the distribution ( $\sigma$ ), and a parameter that allowed the amplitude of the function to vary. To fit the functions, we first "clipped open"

the circular tuning curves for the microstimulation effect and for the visual responses and plotted each on linear axes. We used a fitting algorithm based on chi-square minimization. Errors on the microstimulation data points were calculated from the model parameter estimates ( $\beta_{1-6}$ ) by using the delta method for calculating asymptotic distributions [Y. M. M. Bishop, S. E. Feinberg, P. W. Holland, *Discrete Multivariate Analysis* (MIT Press, Cambridge, MA, 1975)]. For the visual response data, errors were calculated on the basis of the standard deviation of the mean firing rate in a particular direction across eight trials.

32. For this analysis, we estimated the size of each effect by calculating the proportion of decisions changed by microstimulation.
33. The mean multiunit neuronal bandwidth in the significant experiments was 61.7 degrees. This is similar to a mean single-unit bandwidth of 66.0 degrees measured in MT with the same stimuli ( $n = 163$  cells) (K. H. Britten and W. T. Newsome, unpublished data).
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