

Microstimulation of visual cortex affects the speed of perceptual decisions

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Direction-selective neurons in the middle temporal visual area (MT) are crucially involved in motion perception, although it is not known exactly how the activity of these neurons is interpreted by the rest of the brain. Here we report that in a two-alternative task, the activity of MT neurons is interpreted as evidence for one direction and against the other. We measured the speed and accuracy of decisions as rhesus monkeys performed a direction-discrimination task. On half of the trials, we stimulated direction-selective neurons in area MT, thereby causing the monkeys to choose the neurons' preferred direction more often. Microstimulation quickened decisions in favor of the preferred direction and slowed decisions in favor of the opposite direction. Even on trials in which microstimulation did not induce a preferred direction choice, it still affected response times. Our findings suggest that during the formation of a decision, sensory evidence for competing propositions is compared and accumulates to a decision-making threshold.

In our daily life, we must often decide among options on the basis of information we receive through our senses. Such information may be imperfect, unreliable or contaminated by noise. We therefore weigh the available evidence in order to reach the best solution in a reasonable time frame. A central goal of cognitive neuroscience is to understand the neural mechanisms underlying the transformation of sensory signals to a decision. Psychologists have made important inroads^{1–6}, but only recently have neurophysiologists begun to address how such processes are actually implemented in the brain^{7–12}.

By training nonhuman primates to perform difficult visual discrimination tasks, it has become possible to examine the neural basis of decision-making. A useful task for studying the formation of decisions is shown in Fig. 1a. The monkey is trained to judge the direction of motion in a dynamic display of random dots^{13–15}. The difficulty of the discrimination is controlled by adjusting the fraction of random dots that move coherently in one direction or the other (see Methods), so that often decisions must be rendered on the basis of weak sensory evidence. Under such conditions, it has been shown that performance benefits from the accumulation of sensory information in time^{16,17}. Indeed, when monkeys are allowed to control the viewing duration, they take longer to reach a decision when the motion information is weak than when it is strong and the decision is easy¹⁸.

A substantial body of evidence indicates that direction-selective neurons in the middle temporal visual area (MT or V5) represent the sensory information upon which monkeys base their direction decisions in the motion-discrimination task^{14,19–21}. These neurons form an orderly map-like representation of motion: nearby neurons encode similar directions of movement in the same part of the visual field²². However, it is not known how this representation is read out by the rest of the brain in order to reach a categorical decision about direction.

To study this question, we perturbed the activity of neurons in area MT by stimulating with weak currents (see Methods). It has

been shown previously that microstimulation of direction-selective neurons in area MT can bias monkeys' judgments of motion direction in favor of the direction preferred by neurons near the tip of the stimulating electrode¹⁹. This observation offers convincing evidence that the spike discharge of MT neurons plays a causal role in the decision process. To understand how, we extended the direction-discrimination task in a way that permits measurement not only of the monkeys' direction choices but also the amount of time used to reach a decision. Measurement of response time (RT) offers additional insight into the brain processes that link sensory information with decision formation and action^{2–5}. Despite its promise, the combination of RT and threshold sensitivity measurements has rarely been used to study perception³, and it has only recently been tried in nonhuman primates^{18,23}. We found that microstimulation affected both the monkeys' choices and the time taken to reach a decision. These findings suggest that the brain accumulates a difference in the number of action potentials from MT neurons with opposite direction preferences. A decision is made when this accumulated difference reaches a criterion.

RESULTS

Two rhesus monkeys were trained to report the direction of motion in a dynamic random-dot stimulus. We began our experiments by identifying the receptive field and direction preference of the neurons near the tip of our recording/stimulating microelectrode in area MT (Fig. 1a; see Methods). We then had the monkey perform the discrimination task shown in Fig. 1a. The position of the dynamic random dot stimulus was chosen to optimally activate the neurons near the stimulating electrode, and the direction of net random dot motion was either in the preferred direction or in the opposite ('null') direction for these neurons. In half of the trials, microstimulation was applied during motion viewing. Importantly, the duration

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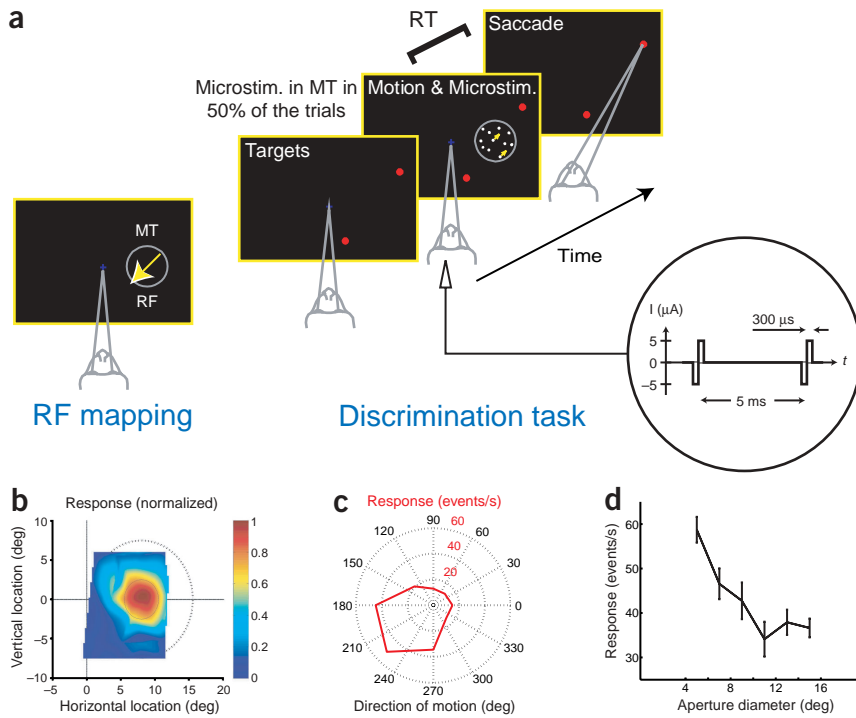


Figure 1 Experimental design. **(a)** Monkeys discriminated the direction of motion in a dynamic random dot display. The direction was in the preferred or null direction of neurons near the tip of the electrode used for microstimulation. The monkey indicated its choice of direction by making a saccadic eye movement to one of two choice targets (red spots) along the axis of net motion. The monkey was allowed to take as little or as much time as needed. Electrical microstimulation was applied on half of the trials as indicated. Both the visual and electrical stimuli were stopped when the monkey's eyes left the fixation window. RF, receptive field; RT, response time. **(b)** Example of the multiunit receptive field map for one site. Color indicates the strength of response to motion in the preferred direction. The thin circles show the size of smallest and largest stimuli used to ascertain center-surround organization in **d**. **(c)** Direction tuning of the multiunit activity at one site. The level of activity is plotted as a function of motion direction in polar coordinates. This site shows a preference for motion down and to the left. **(d)** Surround suppression. The multiunit activity was suppressed by stimuli larger than the area of excitation. This surround suppression was present in all of the sites reported here.

of motion viewing was controlled by the monkey. That is, whenever ready, the monkey made a saccade to one of two choice targets to indicate its decision. We examined the effect of microstimulation on the monkeys' choices and on response time.

On both stimulated and non-stimulated trials, stronger motion in the preferred direction (positive coherence values) led to an increased probability of a preferred direction choice, whereas stronger motion in the null direction (negative values for coherence) led to a decreased probability of a preferred choice (Fig. 2a,b). It has been shown that microstimulation of direction-selective neurons in area MT can cause the monkey to choose the preferred direction more often¹⁹. We confirmed this result in the RT version of the discrimination task. In 15 out of 20 stimulation sites, visual stimuli accompanied by microstimulation were more likely to be judged as moving in the preferred direction of the stimulated neurons ($P < 0.01$; Methods). Our analyses are based on these 15 experiments, which represent a wide variety of receptive field eccentricities and preferred directions of MT neurons.

Two features of the choice behavior are notable. First, the effect of stimulation can be viewed as a shift of the psychometric function to

the left (Fig. 2a,b), suggesting that microstimulation mimics the addition of coherent motion in the preferred direction of neurons near the stimulating electrode. Second, even in these 15 experiments with significant stimulation effects, microstimulation did not always cause the monkey to choose the preferred direction. The monkeys chose the null direction on approximately one-third of stimulated trials (33% and 36% for monkeys B and N, respectively). By examining response time, we aimed to discern an effect of microstimulation on the decision process, even when it did not induce a preferred direction choice.

Monkeys, like humans, make faster decisions in the face of stronger evidence that contributes to certainty. This trend is apparent in the chronometric functions of RT versus motion strength (Fig. 2c,d). On both stimulated and non-stimulated trials, RT was faster for strong motion in either direction and was slowest at low

Figure 2 Microstimulation affects choice and response times. **(a,b)** Effect of random dot motion strength and microstimulation on the monkeys' choices. The probability of choosing the preferred direction of neurons near the electrode tip is plotted as a function of motion strength. Positive and negative motion strengths indicate motion in the preferred and null directions, respectively. The sigmoid curves are fits using equation (1), which characterizes the microstimulation effect as a horizontal shift of the psychometric function. Data are pooled from five experiments (3,544 trials) using monkey B and ten experiments (6,693 trials) using monkey N. **(c,d)** Effect of random dot motion strength and microstimulation on response times. Average RTs (\pm s.e.m.) are plotted as a function of motion strength. Lines are fits using equation (2), which characterizes the microstimulation effect as a horizontal shift of the chronometric function. Only correct choices are shown. Microstimulation caused the monkeys to reduce RT on preferred direction choices and prolong RT on null direction choices.

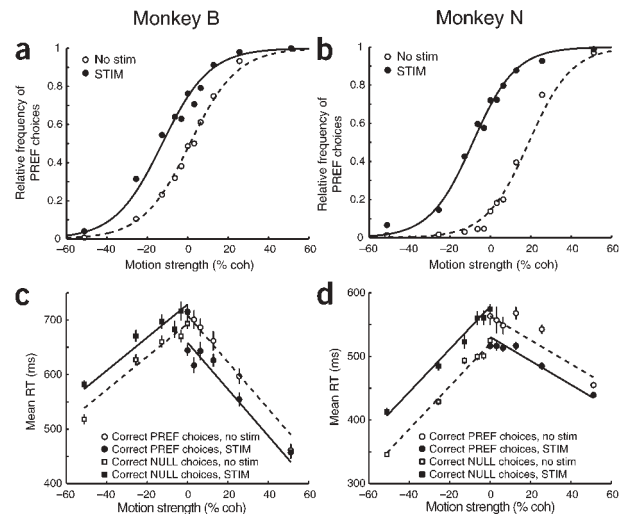
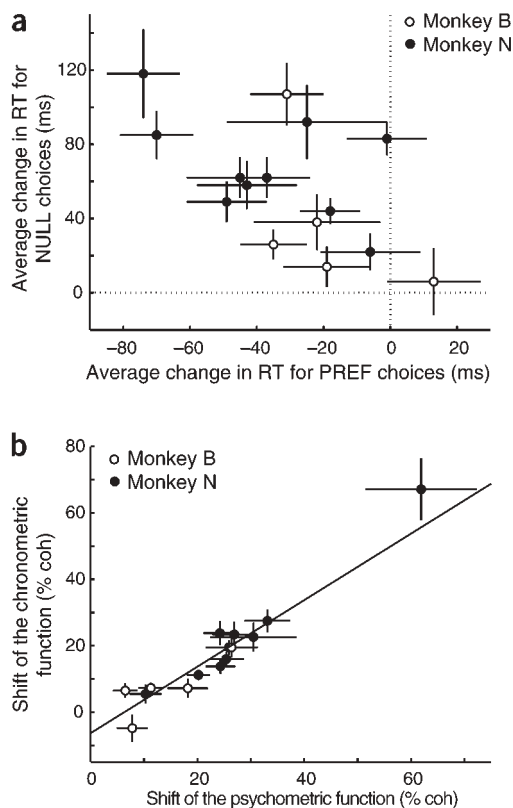


Figure 3 Effect of microstimulation on response time and choice at different electrode sites. **(a)** Comparison of stimulation effects on RT for preferred- and null-direction choices. The plot shows the microstimulation-induced change in RT (\pm s.e.m.), averaged across motion strengths. Stimulation prolonged RT on null direction choices at all sites and decreased RT on preferred direction choices at all but one site. The size of these changes was correlated in individual experiments ($r = -0.58$, $P = 0.02$, Fisher z). **(b)** Comparison of stimulation effects on choice and RT. The equivalent motion strength (\pm s.e.m.) derived from the chronometric functions using equation (2) is plotted against the equivalent motion strength (\pm s.e.m.) derived from the psychometric functions using equation (1). The estimates are strongly correlated (slope = 1.00 ± 0.14 ; $P < 10^{-5}$; H_0 : slope = 0), although estimates from RT were smaller on average (y -intercept: $i = -6.3 \pm 2.9\%$ coherence; $P = 0.05$; H_0 : $i = 0$).

values of motion strength (middle of the abscissa). Microstimulation affected the response times in different ways, depending on whether the monkey chose the preferred or null direction. When the monkeys chose the direction preferred by the neurons at the stimulation site, RT was faster on average (monkey B: 39 ± 8 ms, $P < 10^{-6}$, 3,544 trials from five stimulation sites; monkey N: 37 ± 5 ms, $P < 10^{-6}$, 6,693 trials from ten sites). In contrast, when the monkeys chose the null direction, RT was slower on average (monkey B: 44 ± 7 ms, $P < 10^{-6}$; monkey N: 58 ± 4 ms, $P < 10^{-6}$). On these null-choice trials, microstimulation did not induce the monkeys to choose the preferred direction, yet it retarded the decision process. This pattern of results was seen in all but one of the stimulation sites in our data set, as indicated by the predominance of points in the upper-left quadrant in Fig. 3a. In more than half of the sites, both speeding and slowing effects were statistically significant ($P < 0.01$).

This pattern of results is consistent with the idea that microstimulation acts like the addition of random dot motion in the preferred direction of the stimulated neurons. Based on the monkeys' psychometric functions, we deduced that microstimulation mimicked the addition of $13.7 \pm 1.3\%$ and $27.7 \pm 1.2\%$ coherent motion for monkeys B and N, respectively. This can be seen as a horizontal separation between the two sigmoid functions (Fig. 2a,b). The effect of microstimulation on the chronometric functions can also be approximated by a horizontal shift along the abscissa (Fig. 2c,d). Based on the RT measurements, we deduced that microstimulation mimicked the addition of $11.6 \pm 1.4\%$ ($P < 10^{-6}$; null hypothesis (H_0), $\alpha_4 = 0$ in equation 2) and $17.4 \pm 1.1\%$ ($P < 10^{-6}$) coherent motion for monkeys B and N, respectively. Examination of individual stimulation sites reveals that the magnitudes of the stimulation effect ascertained from choice and RT were highly correlated (Fig. 3b; $r = 0.97$, $P < 10^{-6}$, Fisher z). The systematic relationship between the effect of microstimulation on choice and RT provides clear evidence that the



signals in MT contribute to a common mechanism that explains both decisions and decision times.

The idea that microstimulation affects decisions and decision time through a common mechanism also explains the RT pattern seen on error trials. For weak motion in the null direction, the monkeys occasionally chose the preferred direction in error. Microstimulation caused the monkeys to make more of these preferred-choice errors and to make them faster than on non-stimulated trials (Fig. 4a; mean difference, 102 ± 16 ms; $P < 10^{-6}$, two-way ANOVA; combined data from both monkeys, 870 trials). In contrast, null-choice errors were less frequent during stimulation, and these errors were prolonged in comparison to non-stimulated trials (Fig. 4b; mean difference, 45 ± 10 ms; $P = 10^{-5}$; 1,034 trials). Thus, microstimulation affected the RT on error trials in the same way that was observed for correct choices: it accelerated preferred direction choices and slowed null direction choices.

If microstimulation changed the evidence upon which the decision is based without altering the decision process itself, we should be able to identify a relationship between the psychometric and chronometric data which

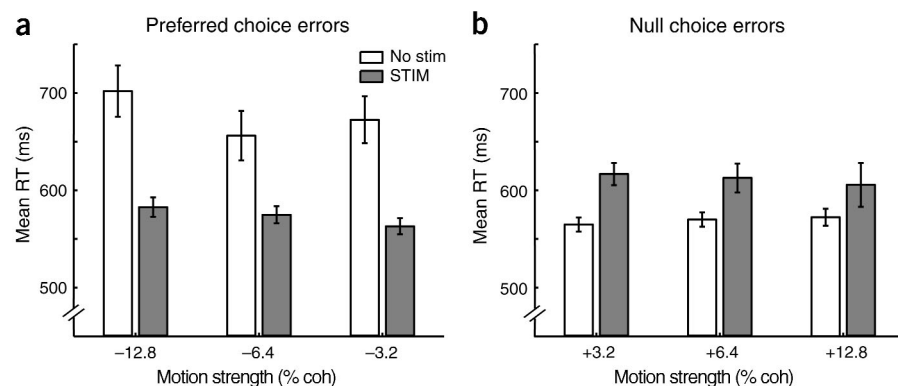
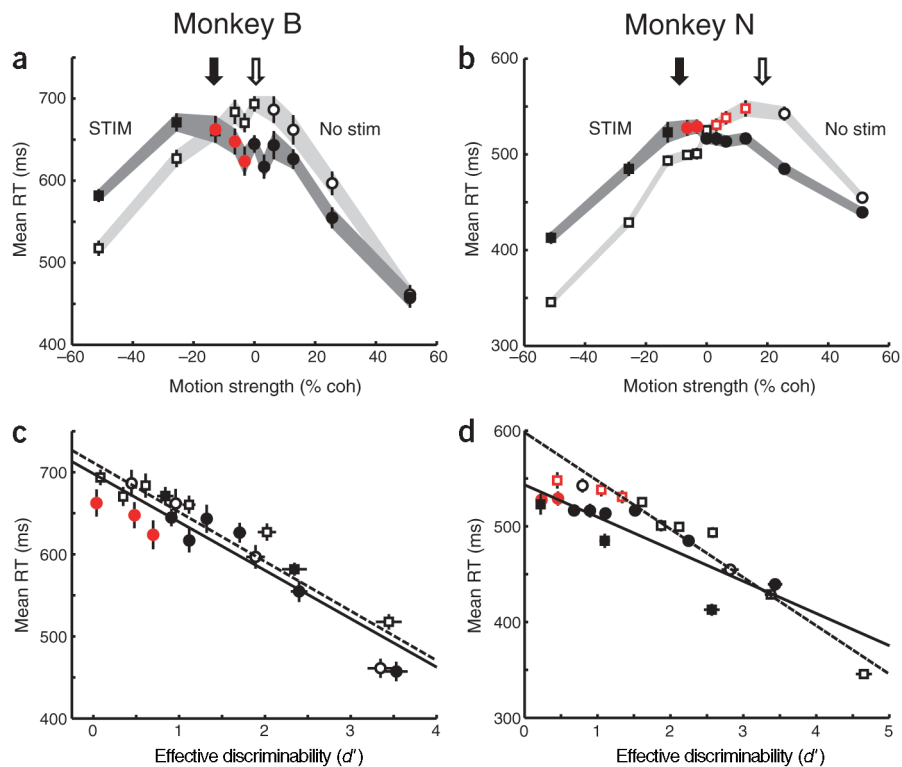


Figure 4 Effect of microstimulation on error response times. Mean RTs (\pm s.e.m.) are plotted for different motion strengths. Note that a preferred direction choice is an error when motion coherence is negative. A null direction choice is an error when the motion coherence is positive. **(a)** Microstimulation caused faster preferred-choice errors. **(b)** Microstimulation caused slower null-choice errors.

Figure 5 Response times reflect effective difficulty or net uncertainty. (**a,b**) Mean RTs (\pm s.e.m.) for stimulation and non-stimulation trials are plotted as a function of motion strength. Positive and negative coherence values correspond to preferred and null directions of the stimulated neurons, respectively. Preferred and null direction choices are grouped together in a single curve. The RT plotted for each motion strength corresponds to the direction choice that the monkey favored in the experiment. Arrows indicate the coherence value that is most ambiguous to the monkey, as ascertained from the sigmoid functions in **Fig. 2a,b**. Points to the right and left of the arrow correspond to preferred and null direction choices, respectively. Some combinations of choice and direction represent errors (red symbols). Open symbols, no stimulation; filled symbols, stimulation; circles, preferred direction choices; squares, null direction choices. The longest RT occurred when the decision was most ambiguous (near the arrows). (**c,d**) RT varies inversely with effective discriminability. The graphs in **a** and **b** have been transformed along the abscissa. Each stimulus/stimulation combination gives rise to a level of accuracy (probability correct) that implies a level of discriminability, d' . Conditions that are least compelling to the monkey (near the arrows in **a** and **b**) are presumed to arise when the signals upon which the decision is based are hardly discriminable (d' near 0). Conditions that are more compelling to the monkey arise when the underlying signals are highly discriminable (large d'). The conversion from probability correct to d' (\pm s.e.m.) is explained in Methods. Symbol conventions are the same as in **a** and **b**. The solid and dashed lines are fits to the stimulation and non-stimulation data, respectively.



holds regardless of whether stimulation has been applied or not. One simple idea is that the time required to reach a decision depends on how compelling the monkey finds the evidence. Whatever combination of motion, electrical stimulation and bias causes the monkey to reach a choice, the process ends sooner when the effective evidence is more compelling. This is readily apparent in **Fig. 5a** and **b**: these graphs group together in a single curve the RT obtained for null direction choices when these were more frequent (left of arrow) and preferred direction choices when these were more frequent (right of arrow). The arrows show the motion strength that the monkey has deemed to be the least compelling; it is the point on the psychometric function (**Fig. 2a,b**) where preferred and null direction choices are equally probable. The maxima of the inverted U-shaped curves fall near these arrows. Thus, the longest RT occurred when the monkey was least certain about direction based on the sensory evidence: when the motion coherence was near zero (monkey B, no-stim. curve), when null direction motion was cancelled by electrical stimulation (both monkeys, stim. curves) or when preferred direction motion was offset by a bias in favor of the null direction (monkey N, no-stim. curve). A change in the motion strength away from the value that the monkey deems most ambiguous adds evidence that the monkey finds more compelling, thereby producing faster decisions. This observation applies to both correct choices (black symbols) and errors (red symbols) seen on stimulated and non-stimulated trials.

Put simply, the monkeys took less time to make a decision when the combination of motion, microstimulation and bias reduced uncertainty about direction. We can appreciate this more directly by examining RT as a function of the monkey's own expression of difficulty. In **Fig. 5c,d**, we replotted each of the points in the inverted Us after transforming the motion strength into a measure of effective

discriminability (d') based on the monkey's own psychometric function (Methods). These d' values serve to estimate the effectiveness of evidence furnished by motion \pm microstimulation. The transformed plots suggest that decisions based on the same effective evidence require a similar amount of time. For monkey B, the relationship between RT and d' was nearly identical for stimulated and non-stimulated trials (**Fig. 5c**; $P = 0.58$). For monkey N, RT was slightly faster on stimulation trials, especially when the effective evidence was weak (**Fig. 5d**; $P = 0.002$). This observation can be explained if the microstimulation had activated not only neurons tuned to the preferred direction but also neurons that prefer the null direction, thereby adding both signal and noise to the decision process. Such 'noise' would weaken the effective evidence, but for reasons that will be explained below, it should speed the decision process. The important point from **Fig. 5** is that a common process that combines evidence from the visual stimulus and microstimulation seems to explain both decisions and decision time.

DISCUSSION

It appears that the neurons stimulated in our experiments affect the decision process in three ways. First, as shown previously, they cause the monkey to choose the preferred direction more often. Second, they cause the monkey to choose this direction more quickly. Third, they cause the monkey to choose the null direction more slowly.

This third observation is especially informative. It indicates that microstimulation is not ignored on trials in which the monkey does not choose the preferred direction of the stimulated neurons, and it shows that neurons that prefer one direction participate in the decision process even when the outcome is the opposite direction. Based on previous experiments that examined choices but not RT, it was

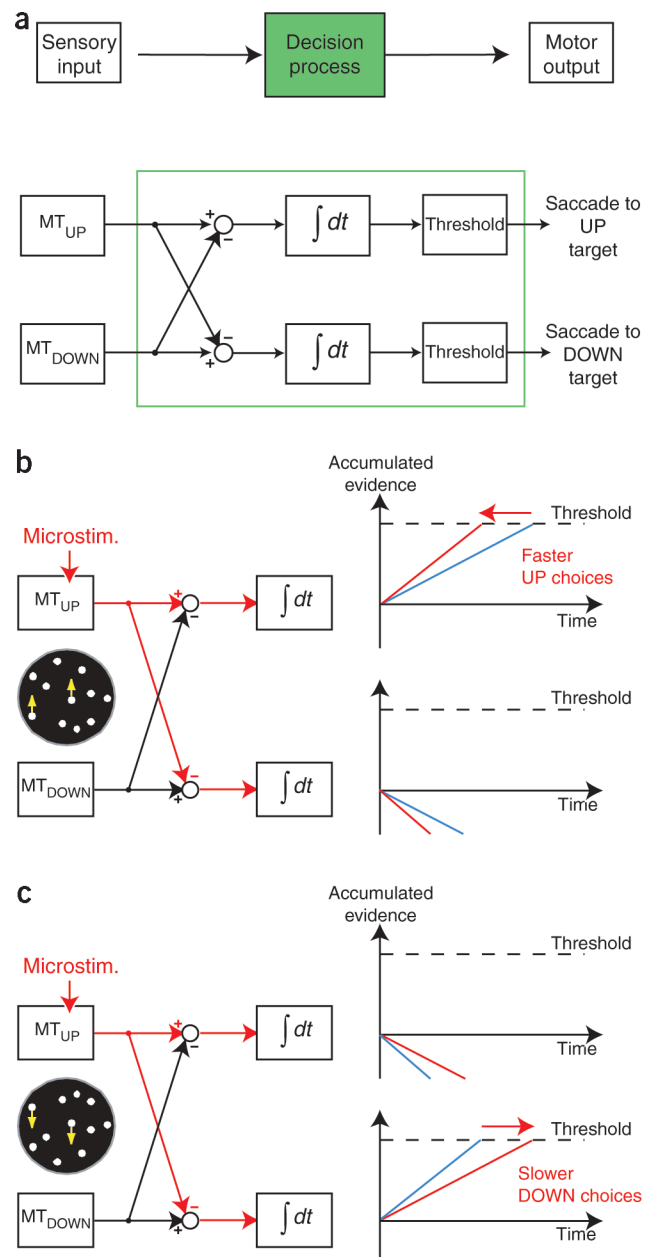
Figure 6 Model of the decision process. The diagram depicts up versus down decisions, and assumes that neurons near the stimulating electrode prefer upward motion. (a) Evidence for upward consists of a comparison of upward- and downward-preferring sensory signals. Evidence for downward consists of the opposite comparison. The differences are integrated as a function of time, and the accumulations are compared to threshold. The evidence that first reaches threshold governs the choice and decision time. (b) An upward choice occurs because the evidence for upward is first to reach threshold (blue lines). Microstimulation of upward-preferring neurons increases the rate of this accumulation (red lines), thereby increasing the likelihood of an up choice and reducing the decision time. The downward ramps depict the developing activity in the integrator for downward choices, which does not win the race. (c) A downward choice occurs because the evidence for downward is the first to reach threshold (blue lines). Microstimulation of upward-preferring neurons decreases the rate of this accumulation (red lines), thereby reducing the likelihood of a down choice and increasing decision time. The downward ramps depict the developing activity in the integrator for upward choices, which does not win the race.

suspected that microstimulation might override the natural decision process on some fraction of trials^{19,24}. In contrast, we propose that microstimulation adds information to the decision process, even when it fails to cause a preferred direction choice: its imprint on the process is revealed by the RT.

These results support a relatively simple model for the decision process that underlies performance on this task (Fig. 6a). The model is illustrated for the case of a discrimination between up and down motion. Two processes accumulate evidence in favor of upward and downward motion, respectively. The choice and corresponding response time are determined by the first process to accumulate evidence to a threshold level. The idea that the decision terminates when a value reaches a criterion level is a common feature in several models of decision formation^{3,4,6,25} and motor reaction time^{26,27}. The critical feature of the model in Fig. 6a is that the evidence derives from a comparison of responses from direction-selective sensory neurons in area MT. The evidence for upward is the difference between upward and downward preferring neurons; the evidence for downward is the opposite difference. When motion is strong, this difference tends to be large, and choices are made rapidly. When motion is weak, the difference is small and variable in sign; thus choices are slower and often incorrect. Even when the opposing motion signals are balanced, the moment-to-moment variability allows the accumulated 'evidence' to wander toward threshold, analogous to Brownian motion. Thus, larger amounts of variability (*i.e.*, noise) would be expected to reduce accuracy and cause faster threshold crossings.

The model explains the effect of microstimulation on both choice and RT. Stimulation of upward neurons increases the evidence for upward and decreases the evidence for downward. The result is a greater tendency for the upward process to win the race to threshold and for it to do so earlier (Fig. 6b). When the downward process wins, it does so more slowly as a result of the disadvantage conferred through activation of upward neurons (Fig. 6c). The model therefore predicts that RT should be slowest when choices are most uncertain, whether such uncertainty arises because of weak visual motion or the combination of motion and microstimulation. This prediction is supported by the analysis in Fig. 5.

The key feature of the model is that MT neurons with opposite directional preferences must contribute in an opponent fashion to both upward and downward decisions. If down decisions were based solely on information from downward-preferring sensory neurons, then stimulation of upward MT neurons would not retard downward decisions. In fact, without opponency, we should have



observed faster down responses, because our data would contain only those downward decisions that could win the race against the accelerated upward process.

Where in the brain does this putative differencing operation take place? We think it is unlikely to be mediated by inhibitory (opponent) interactions between neurons in area MT. First, there is little evidence for inhibitory interactions between neurons in MT with opposite directional preferences. Although motion in a neuron's null direction can suppress responses to motion in the preferred direction²⁸, the mechanism of this suppression involves neurons with smaller receptive fields, presumably at the level of primary visual cortex^{29,30}. Second, for the random dot stimuli used in our experiments, nearly all neurons in MT actually increase their response when stimulated with random dot motion in their null direction, especially over the range of motion strengths used in our study³¹. In other words, MT neurons respond as if low coherence motion in their null direction provides net

excitation, albeit weaker than the excitation provided by motion in the preferred direction. Thus, inhibitory interactions between neurons in MT appear to be too weak to account for the nearly symmetrical effect of microstimulation on the monkeys' decisions for and against the direction preferred by the stimulated neurons.

Several lines of evidence suggest that the directional signals in area MT are at most weakly opponent, but are often read out in an opponent manner to produce perception and behavior. For example, it is known that the sum of two sinusoidal gratings moving to the left and right, respectively, produces activity in both leftward and rightward MT neurons²⁸. Yet, the sum does not appear as two patterns moving past each other, but as a stationary, flickering grating^{32–34}. On the other hand, when two sparsely textured patterns move over one another in opposite directions, they also produce activity in opposing MT neurons^{30,35}, yet the perception is of two transparent textured surfaces moving in opposite directions. These observations suggest that a mechanism downstream of MT can compare the two opposing motion signals from MT. This comparison stage is likely to be mediated by higher-level brain structures, which are capable of inferring stationary flicker or transparency based on other visual cues.

Furthermore, although opponent interactions between motion sensors have long been thought to explain the effects of motion adaptation³³, this opponency is not explained by inhibitory interactions within MT. According to a recent study, prolonged exposure to rightward motion causes a reduction in response from rightward preferring MT neurons, but it does not enhance the response of leftward preferring neurons³⁶. The finding indicates that leftward and rightward MT neurons do not suppress each other appreciably. To explain the perceptual consequences of adaptation, it is necessary to compare leftward and rightward responses using structures downstream of MT. Finally, recent recordings of MT neurons during an apparent motion eye tracking task suggest that the pursuit eye movement system obtains its estimate of velocity by comparing the responses of MT neurons with opposite direction preferences³⁷.

It is likely that the differencing operation shown in our results is calculated in brain structures that read out or interpret the sensory signals from MT. Neurons in the posterior parietal cortex^{15,18}, superior colliculus³⁸, frontal eye field and prefrontal cortex³⁹ show ramp-like changes in their discharge, which resemble the idealized traces in Fig. 6b and c. Whereas neurons in MT show an increase in spike rate for both preferred- and null-direction stimuli, neurons in these downstream 'read out' areas increase or decrease their spike rate in accordance with the weight of evidence that leads to the monkeys' decision. Indeed, the ramp-like activity of neurons in the lateral intraparietal area (LIP) has been shown to correlate with both the decision and response times in the same two monkeys studied here¹⁸.

While details concerning the circuitry await further clarification, the present result teaches us how the brain interprets the signals produced by sensory neurons. To decide between two alternatives, the responses of neurons with opposing preferences are compared to obtain net evidence for one alternative versus the other. The sign of the difference indicates which alternative is more likely; the magnitude of the difference reflects the persuasiveness of the evidence³. It has been shown that such a difference in spike rates is proportional to the logarithm of the likelihood ratio (or weight of evidence) in favor of a proposition^{40,41}. Therefore, as a statistic, it has properties that are known to be useful for weighing the merits of one hypothesis against another, especially when integrated over time^{40,42}. Our result provides direct experimental support for such a computation in the brain. It suggests that sensory neurons do not act as labels for their favorite stimuli but rather as sources of evidence, which can be inter-

preted as for or against a proposition about the state of the environment, or equivalently, for or against a particular behavioral response¹⁶. It remains to be seen whether this framework applies to the read-out of sensory signals in more complicated settings.

METHODS

Monkey preparation. Two adult female rhesus monkeys (*Macaca mulatta*) weighing 4.5–6 kg were subjects in the experiments. Details of surgical, training and recording procedures have been previously published¹⁸. Briefly, a head-holding device, scleral search coil for monitoring eye position and recording chamber were implanted under general anesthesia. The location of recording/stimulation sites in area MT was determined from physiological properties of MT neurons and confirmed based on examination of high-resolution MRIs which were registered with a surface-based atlas using the CARET software package^{43,44}. All surgical and experimental procedures were in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals and were approved by the University of Washington Animal Care Committee.

Characterization of stimulation sites. During the experiment, the monkey was seated in a primate chair with head fixed. Visual stimuli were presented on a computer monitor (viewing distance, 60 cm) using the Psychophysics Toolbox extension of MATLAB^{45,46}. Tungsten microelectrodes suitable for multi-unit recording and stimulation were advanced into area MT (FHC; impedance >0.75 M Ω before stimulation and ~0.5 M Ω after). We recorded multi-unit activity by setting a voltage threshold just above the level of background activity. The multi-neuron response was quantified by the average rate of threshold crossings during presentation of the visual stimulus (events/s in Fig. 1). We used this activity to characterize the receptive field size, location and directional tuning of the neurons near the tip of the recording electrode. We ensured that these properties remained consistent for ± 100 μ m along the electrode track. The range of receptive field eccentricities included in this paper was from 3.0° to 9.8° (median, 7.1°). Receptive field diameters (at half the maximum response) ranged from 6.6° to 10.5° (median, 8.0°), and all sites showed some suppression to stimuli that extended beyond the boundary of the classical receptive field. Preferred directions for the 15 sites were approximately uniformly distributed on the circle ($P = 0.60$; Rayleigh test). The properties of a typical stimulation site are shown in Fig. 1b–d.

Task design. Monkeys performed a direction discrimination task (Fig. 1a). They were trained to indicate the net direction of motion in a dynamic random dot display by making an eye movement to one of two choice targets. The difficulty of the direction discrimination was governed by the fraction of dots that were displaced in apparent motion, termed the percent coherence; dot displacement size was adjusted to match the preferred speed of the neurons, typically ~6 °/s. The remaining dots were replaced randomly. The direction and strength of random dot motion was chosen randomly on each trial using the following values: 0, ± 3.2 , ± 6.4 , ± 12.8 , ± 25.6 and ± 51.2 % coherence. Positive and negative values indicate the direction of displacement in the preferred or null direction, respectively. The 0% coherence stimuli contain no net motion on average. For these trials, the monkey was rewarded on half of the trials. Otherwise the monkey received a liquid reward for making an eye movement to the choice target along the trajectory of apparent motion. The task was structured as a one-interval, two-alternative forced choice discrimination task. The monkey was allowed to take as little or as much time as needed to judge the direction of motion. Once the monkey's gaze left the fixation window ($3 \times 3^\circ$ and $2 \times 2^\circ$ for monkeys B and N, respectively), the random dot stimulus was extinguished.

On half of trials (chosen randomly), we stimulated the cortex during the period of motion viewing. Stimulation was controlled by a Grass S88 with optical isolation units (Grass PSIU6). Stimulation trains were biphasic current pulses (± 5 μ A, 300 μ s pulse width; Fig. 1a) delivered at a repetition rate of 200 Hz. The microstimulation began with onset of the random dot motion and was extinguished along with the visual stimulus when the computer detected a break in the monkey's fixation. Microstimulation had no bearing on the provision of reward; the choice was designated correct or incorrect based on the net motion of the random dots. The strategy, which is identical to the one used in an earlier study¹⁹, offers no incentive to respond one way or

another on stimulated trials. In fact, the optimal strategy would be to ignore the microstimulation, were it sensed.

Data analysis. The choice data (Fig. 2a,b) were analyzed using logistic regression, whereby the probability of a preferred direction choice is given by

$$P_{\text{pref}} = \frac{e^Q}{1 + e^Q}, \quad Q = \beta_o + \beta_1 C + \beta_2 I_E \quad (1)$$

where C is motion strength expressed as percentage coherence using the convention that positive and negative values denote motion in the preferred and null direction of the stimulated neurons, respectively. I_E is 1 if electrical stimulation accompanied the trial and 0 otherwise. The β_i are free parameters which were fit using the method of maximum likelihood. The size of the stimulation effect is conveniently expressed in units of equivalent motion strength by taking the ratio β_2/β_1 , corresponding to a left shift in the sigmoid function. Standard errors of parameters were estimated from the Hessian matrix of second partial derivatives of the log likelihood⁴⁷. The analyses shown in Figs. 2–4 are based on 15 (out of 20) sites in which microstimulation clearly biased the monkeys choices in favor of the preferred direction ($\beta_2 > 0, P < 0.01$).

Response times were defined as the interval between onset of random-dot motion and initiation of the saccadic eye movement response. They were analyzed by fitting lines to the RT as a function of motion strength. The model permits separate linear fits for preferred and null direction choices, but it is constrained to represent the effect of microstimulation by the same horizontal shift of these lines.

$$\text{RT} = \begin{cases} \alpha_o + \alpha_1(C + \alpha_4 I_E) & \text{preferred choice} \\ \alpha_2 + \alpha_3(C + \alpha_4 I_E) & \text{null choice} \end{cases} \quad (2)$$

where the α_i are the fitted parameters (maximum likelihood). Notice that stimulation adds the value α_4 to the coherence term. We also report the average change in RT caused by microstimulation. This measure does not rely on a model fit but instead combines the RT changes obtained at each motion strength into a weighted average (e.g., Fig. 3a). Only RTs of correct choices were analyzed.

Comparison of stimulation effects on choice and RT was based on estimates of equivalent motion strength and their standard errors. The linear fit shown in Fig. 3b incorporates uncertainty (standard error) in both x and y variables⁴⁸. Unless otherwise stated, all tests of the null hypothesis (H_0) were t -tests based on the standard error of fitted coefficients.

For the analysis in Fig. 4, we combined data from both monkeys to obtain a sufficient number of error trials at the six motion strengths shown. For each motion strength within this range, at least 25 errors were available on both stimulation and non-stimulation trials.

The estimates of effective discriminability, d' , used in Fig. 5 were obtained using a two-step procedure. We first fitted psychometric functions to the behavioral data using maximum likelihood estimation. The function had one extra degree of freedom compared to the fits shown in Fig. 2:

$$P_{\text{pref}} = \frac{e^Q}{1 + e^Q}, \quad Q = \beta_o + \beta_1 C + \beta_2 I_E + \beta_3 I_E C \quad (3)$$

The additional interaction term allows the slope of the sigmoid functions to differ under stimulation and non-stimulation conditions. The interaction term, β_3 , was -0.015 ± 0.007 ($P = 0.03$; for comparison, $\beta_1 = 0.094$) and -0.031 ± 0.006 ($P < 10^{-6}$; $\beta_1 = 0.111$) for monkeys B and N, respectively. Note that we omitted the interaction term in equation (1) to characterize the microstimulation-induced change as a leftward displacement of the sigmoid. This was a reasonable simplification (see fits in Fig. 2) that allowed us to compare effects across experiments. However, the negative interaction between stimulation

and motion coherence suggests that in addition to acting like preferred direction motion, microstimulation added a small amount of noise to the discrimination process¹⁹, especially for monkey N.

The probabilities furnished by these fits were then converted to d' using

$$d' = \left| \Phi_{0, \sqrt{2}}^{-1}(P_{\text{pref}}) \right|$$

where $\Phi_{0, \sqrt{2}}^{-1}$ is the inverse of the cumulative normal distribution with mean 0 and standard deviation $\sqrt{2}$. d' represents the difference in means between two independent, normally distributed random variables with unit variance such that a pair of random draws, one from each distribution, would show the appropriate ordinal relationship. It is a natural scale for the expression of difficulty⁴⁹. An equally useful alternative would be to use the log odds ratio, which is given by the polynomial exponent Q in equation (3). The standard error of d' was estimated by applying error propagation to the fits to equation (3) and then transforming each $P \pm \text{s.e.m.}$ to obtain a range of $d' \pm \text{s.e.m.}$ (horizontal error bars in Fig. 5c,d). Line fits to the data take uncertainties on both d' and RT axes into account. We used an F -test to determine whether these lines differed for stimulation and no-stimulation conditions.

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COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

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