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A relationship between behavioral choice and the visual responses of neurons in macaque MT

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Abstract

We have previously documented the exquisite motion sensitivity of neurons in extrastriate area MT by studying the relationship between their responses and the direction and strength of visual motion signals delivered to their receptive fields. These results suggested that MT neurons might provide the signals supporting behavioral choice in visual discrimination tasks. To approach this question from another direction, we have now studied the relationship between the discharge of MT neurons and behavioral choice, independently of the effects of visual stimulation. We found that trial-to-trial variability in neuronal signals was correlated with the choices the monkey made. Therefore, when a directionally selective neuron in area MT fires more vigorously, the monkey is more likely to make a decision in favor of the preferred direction of the cell. The magnitude of the relationship was modest, on average, but was highly significant across a sample of 299 cells from four monkeys. The relationship was present for all stimuli (including those without a net motion signal), and for all but the weakest responses. The relationship was reduced or eliminated when the demands of the task were changed so that the directional signal carried by the cell was less informative. The relationship was evident within 50 ms of response onset, and persisted throughout the stimulus presentation. On average, neurons that were more sensitive to weak motion signals had a stronger relationship to behavior than those that were less sensitive. These observations are consistent with the idea that neuronal signals in MT are used by the monkey to determine the direction of stimulus motion. The modest relationship between behavioral choice and the discharge of any one neuron, and the prevalence of the relationship across the population, make it likely that signals from many neurons are pooled to form the data on which behavioral choices are based.

Keywords: Visual cortex, Extrastriate, Middle temporal, Motion sensitivity, Psychophysics, Discrimination, Behavior, Monkey

Introduction

One of the basic problems of neuroscience is to discover the links between the activity of the elements of the nervous system and the behavior of organisms. Over the last few years, we have explored the link between visual cortical activity and perceptual judgment by studying the responses of neurons in area MT (or V5), a region of the macaque extrastriate visual cortex, while monkeys performed a behavioral discrimination task. Our results suggest that MT neurons may provide the signals upon which the behavioral discriminations are based (Britten et al., 1992), and are in good agreement with evidence from a variety of sources that suggests a critical role for MT in visual motion processing (Zeki, 1974; Maunsell & Van Essen, 1983; Albright, 1984; Movshon et al., 1985; Newsome & Paré, 1988; Salzman et al., 1992; Schiller, 1993). Our analysis of this question has concentrated on comparing averaged neuronal responses and behavioral judgments to the same visual stimuli, and using this comparison to deduce functional relationships. In this paper, we turn to the question of how on a particular trial neuronal and behavioral response are related *to each other*, in an effort to understand how sensory signals inform specific perceptual decisions.

In these experiments, we simultaneously measured the responses of single MT neurons and behavioral judgments under conditions in which the stimuli were nearly optimal for the discriminative capabilities of the neurons under study. Both mea-

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surements are variable: under constant stimulus conditions the monkeys' choices will vary from trial to trial, as will the responses of MT neurons. If these neuronal signals form the basis for the perceptual judgments, then neuronal variability should be reflected in behavioral variability. In other words, over a set of identical trials, the activity of the neuron and the monkey should be correlated. Our analysis reveals that, on average, there is such a correlation: the monkeys were more likely to choose the direction preferred by an individual neuron when it fired more strongly. This relationship was not due to variability in the visual stimulus itself, and was only present when the monkey made behavioral choices between visual stimuli whose directions of movement differentially activated the neuron being recorded. Our observations support the idea that this positive correlation is a consequence of the fact that the neuronal signals we recorded contribute directly to the monkey's choice behavior.

Preliminary accounts of these results have appeared elsewhere (Britten et al., 1988; Newsome et al., 1989), as has a report of similar observations in area MST (Celebrini & Newsome, 1994).

Methods

The results reported in this paper are based on a new analysis of data from experiments that we have for the most part described previously. The experimental methods are outlined here, and we refer the reader to our earlier reports for more detailed descriptions (Newsome & Paré, 1988; Britten et al., 1992, 1993).

Subjects and surgery

These experiments were performed on four adult rhesus macaques (*Macaca mulatta*), three male and one female. Three of these monkeys were subjects in previously published physiological experiments (monkeys E, J, and W); the fourth (monkey K) was added later. Each monkey was implanted with a stainless-steel head holder and scleral search coil (Judge et al., 1980), and trained to criterion on a direction discrimination task (see below). A stainless-steel recording cylinder was then implanted over occipital cortex, and recording experiments were initiated. All animal care and surgical procedures conformed with NIH guidelines for the care and use of laboratory animals.

Visual stimuli

The stimuli in these experiments were fields of dynamic randomly positioned dots rapidly plotted (6.67 kHz) on the face of a CRT screen (HP 1321 or Xytron A21, P4 phosphor). The stimulus covered a square 20 deg on a side, but was usually masked down to a smaller area matched to the receptive field of the neuron under study. Each dot was 0.1 deg in diameter and of very high contrast; the average luminance was 0.6 cd/m^2. A specifiable fraction of the dots carried a unidirectional apparent motion signal whose speed was optimal for the neuron under study. We varied the strength of the motion by specifying the probability with which any particular dot would be plotted in apparent motion. The other dots were positioned randomly to create masking motion noise. We give the strength of the stimulus as the proportion of coherently moving dots, here termed the *coherence* of the visual stimulus (in previous reports we have used the term *correlation* for this value). By varying coherence, we were able to measure the sensitivity of both single cells and of monkeys to the same weak, spatially distributed motion signal.

Task and training

We measured psychophysical performance in a two-alternative forced-choice procedure in which eye movements were measured both to ensure correct fixation and to provide the operant response which indicated the choice on a trial. This task is schematically illustrated in Fig. 1. On each trial, the monkey was first required to maintain fixation on a small spot of light, and the trial was terminated if the monkey broke fixation at any time. Once the monkey had maintained fixation for 300 ms, the motion stimulus was turned on within an aperture centered on the receptive field, and remained on for 2 s. The fixation point and stimulus were then turned off and two saccade targets were illuminated, corresponding to the two possible directions of motion, always 180 deg apart. The monkey indicated its choice by making a saccade to one of the two targets. A correct choice

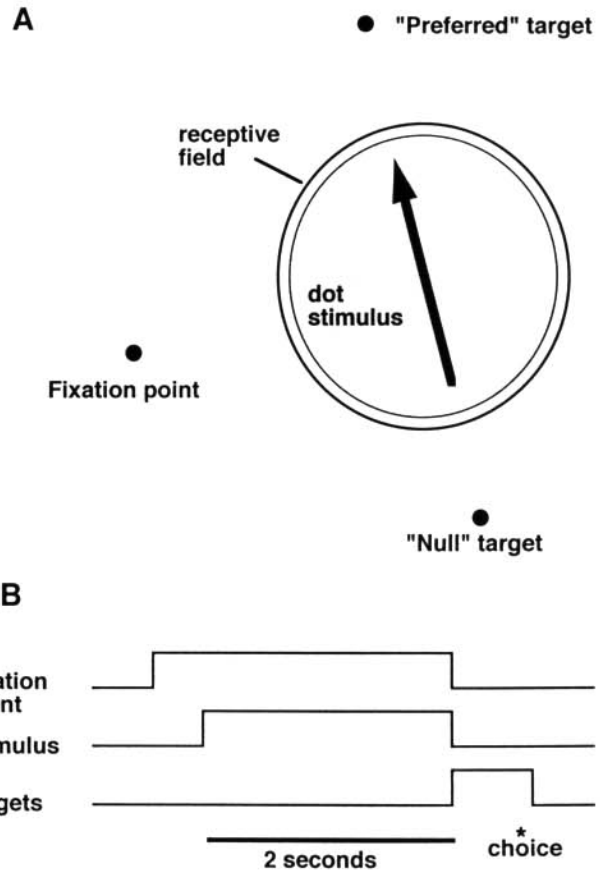

Fig. 1. Schematic of the behavioral task and stimulus configuration used in these experiments. A: Spatial configuration. The outer circle denotes the receptive field of the neuron under study, and the inner shaded region the random dot stimulus. This stimulus can be in either the neuron's preferred direction or its opposite ("null"). Response targets, which were small spots of light from projection LEDs, were aligned with the two possible directions of motion along a diameter of the stimulus. In some circumstances, we would shift these away from collinear alignment to reduce choice biases. B: Timing of events in a trial.

was rewarded with a drop of water or juice, and an incorrect choice was punished with a brief time-out period. Trials were presented in blocks in which the two directions were equiprobable and randomly interleaved, and in which the motion strength was controlled by the method of constant stimuli.

Physiological recording

During each recording session, we introduced single-unit electrodes (10–30 μm tip exposure; Haer, Brunswick, ME, Micro Probe, Clarksburg, MD) into MT until a suitable single unit was isolated. We mapped the receptive field using conventional geometric targets, chose a screen aperture so that the stimulus just filled the receptive field, and established the preferred speed and direction using 100% coherence random dot stimuli. We then presented blocks of trials containing stimuli of several coherence values spanning threshold, moving either in the preferred direction or its opposite (the "null" direction). Typically, 15 trials per condition were presented in each block, and we continued to present blocks of trials as long as isolation could be maintained and the monkey continued to perform the task.

Neuronal data base

We accepted neurons for analysis if they could be held long enough to complete an average of at least seven trials per condition, and if their responses were direction selective. Specifically, we required that the *smallest* response to the preferred direction be larger than the *largest* response to the null direction at the highest coherence tested. This restricted our sample to reliably directionally selective cells, more than 90% of the cells we encountered in MT. Of the 299 neurons described in this paper, 216 were included in previous reports (Britten et al., 1992, 1993). The new data come from 38 cells from monkey K and 45 new cells from monkey E.

Histology

Monkeys E and K are still participating in related experiments; we have histologically confirmed the location of the recording sites in monkeys J and W. Each animal was killed with an overdose of barbiturate and perfused with 0.9% normal saline followed by 10% formalin fixative. The brain was removed, blocked, and allowed to sink in 30% sucrose. Frozen sections of 48-μm thickness were cut in a parasagittal plane, and alternate sections through the area of interest were stained with cresyl violet or myelin by a modified Gallyas method (Gallyas, 1979). The area from which we recorded was always clearly visible from extensive guide tube damage posterior to MT. This region always corresponded well with a heavily myelinated region on the posterior bank of the superior temporal sulcus, the best-known anatomical landmark for MT (Allman & Kaas, 1971; Ungerleider & Mishkin, 1979; Van Essen et al., 1981).

Results

A measure of the association between neuronal response and behavioral judgment

To examine the relationship between neuronal response and behavioral choice, we took advantage of the fact that when our monkeys were presented with stimuli near threshold, they made both "preferred" and "null" direction choices in response to any particular stimulus. This allowed us to consider whether a relationship existed between behavioral choice and neuronal response even under conditions when the stimulus did not vary from trial to trial. To illustrate this relationship, Fig. 2 shows

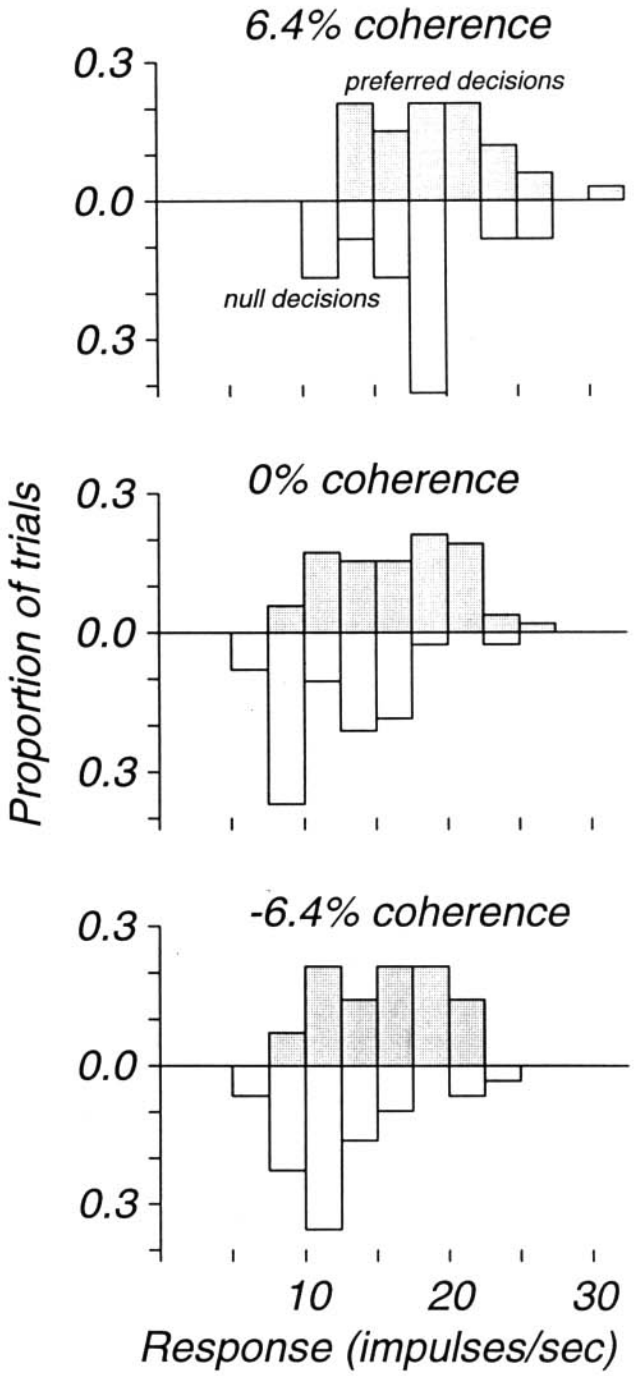

Fig. 2. Response distributions from a representative MT cell which showed a substantial trial-to-trial covariation between firing rate and behavior. Each panel represents a single stimulus coherence and direction; the −6.4% condition corresponds to null direction motion. The upper histograms (stippled) show firing rates on trials on which the monkey decided in favor of the preferred direction, and the lower histograms (open) show the firing rates on trials on which the monkey made the opposite decision.

the responses of an MT neuron whose discharge was related both to the stimulus and to the monkey's behavioral choice. Each pair of histograms shows two distributions of firing rates for the responses of this neuron to a single stimulus type. The pair in the upper panel shows responses to motion in the preferred direction at 6.4% coherence. The pair in the middle panel shows responses to 0% coherence, and the pair in the lower panel shows responses to motion in the null direction at 6.4% coherence. The relationship between the visual stimulus and response can be seen in the trend for average responses to increase from the bottom to the top of the figure. The relationship between the monkey's choice and response can be seen in each panel: the upper, stippled histogram shows the distribution of responses on trials on which the monkey judged the motion to be in the neuron's preferred direction, while the lower, unfilled histogram shows the distribution of responses on trials on which the monkey judged the motion to be in the neuron's null direction. For all three stimulus conditions, the upper histogram is shifted to the right with respect to the lower one, showing that the neuron fired more strongly on trials on which the monkey made decisions in favor of the neuron's preferred direction. This shift was significant for each of the lower two pairs (t-test, $P < 0.01$).

To avoid distributional assumptions inherent in the t-test, we elected to use a nonparametric statistic to examine the reliability of this effect. We devised a method based on signal detection theory, which is analogous to the receiver operating characteristic (ROC) analysis that we and others have used previously to describe neuronal responses (Green & Swets, 1966; Barlow et al., 1971; Cohn et al., 1971; Tolhurst et al., 1983; Bradley et al., 1987; Vogels & Orban, 1991; Britten et al., 1992). For each pair of distributions like those shown in Fig. 2, we calculated an operating characteristic in a manner identical to ROC analysis; the area under such a curve (not shown) captures the amount of overlap of the distributions (Green & Swets, 1966; Bamber, 1975). The values for the three pairs of distributions shown in Fig. 2 are 0.57, 0.78, and 0.75.

The simplest way to conceptualize these values is as the probability that, given one draw from each distribution, the value from the preferred-choice distribution would be larger. Suppose we were given data from two trials, on one of which the monkey made a "preferred" choice and the other of which the monkey made a "null" choice, but that we were not told which trial was which. Our measure gives the probability that an observer, given only the firing rates for two trials, would be able to identify accurately which of the trials led to the monkey making each choice. A value of 0.5 of course represents chance performance, and a value of 1.0 represents a perfect association between neuronal and behavioral response, whose sense is such that the monkey's choice corresponds to the neuron's preferred direction. We term this value *choice probability*, to emphasize its status as an indicator of the accuracy with which neuronal response predicts the monkey's choice. We calculated choice probability for all stimulus conditions under which the monkey made at least three correct and three incorrect decisions.

For each cell the choice probability appeared to be independent of the stimulus coherence or of the magnitude of the neuron's response. We evaluated these impressions in two ways. First, we averaged the choice probability measurements for each coherence level across all of the tested cells, and the results are shown in Fig. 3A. Choice probabilities were modestly but reliably affected by stimulus direction (analysis of covariance: $F = 4.3$, $df = 2,2667$, $P = 0.014$), but not by the coherence of the stimulus ($F = 2.4$, $df = 1,2668$, $P = 0.14$). This suggests that the strength of the stimulus, and by extension the strength of the neuron's response, should not have a consistent effect on choice probability. Fig. 3B shows a direct examination of this question, in which we plot the calculated choice probability for each of 2668 stimulus conditions for 299 neurons as a function of response magnitude. The superimposed jagged curve is a moving average of 41 adjacent observations. There was no strong relationship between mean neuronal response and choice probability, as long as the firing rate was greater than 1–2 impulses/trial. We cannot be sure why the choice probability collapsed to 0.5 for these very weak responses, because the reliability of the measure is probably poor when the spike counts become very low.

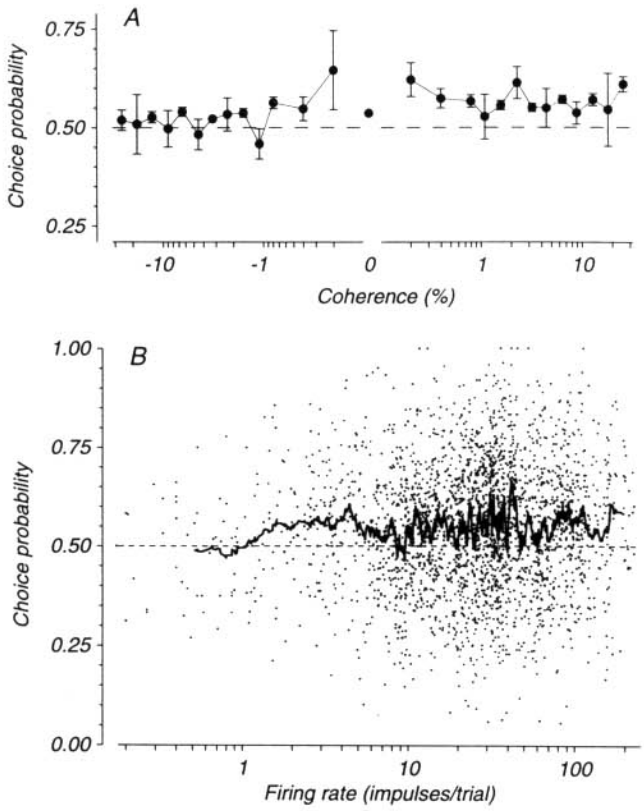

Fig. 3. Dependence of choice probability on stimulus coherence and neuronal response. A: The average relationship between stimulus coherence and choice probability for all 299 cells in our sample. Negative coherence values indicate null direction motion. Each point represents the average choice probability for all cells for which a choice probability could be measured at that coherence level. The error bars represent the standard error of the mean; large errors typically mean that the coherence level was rarely employed in our experiments. B: The relationship between mean neuronal firing rate and choice probability for 2668 stimulus conditions for the 299 cells in our sample. Each point represents the calculated choice probability for a single stimulus. The jagged line shows the running mean of 41 adjacent observations.

It is of interest to know how this measure relates to more conventional measures of neuronal response such as changes in firing rate. Fig. 4 shows the relationship between choice probability and the ratio of responses measured for trials on which the monkey made correct and incorrect behavioral judgments, for the same 2668 stimulus conditions and 299 neurons as in

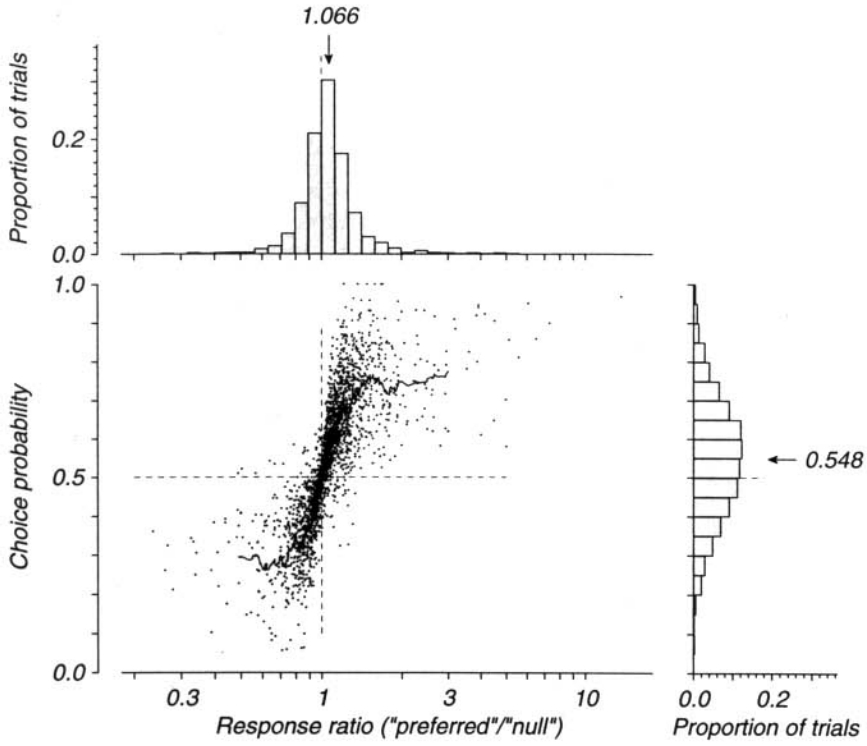

Fig. 4. The relationship between choice probability and firing rate ratios between preferred and null choice trials, for the same set of observations shown in Fig. 3B. The marginal distributions show the distribution of each measure, and the arrows indicate the corresponding means. The jagged line is a running mean of 41 adjacent observations.

Fig. 3B. The abscissa shows the ratio of the firing rates measured for the two choice conditions, and the ordinate shows the choice probability for the same stimulus condition. As in Figs. 3A and 3B, each stimulus condition was analyzed separately. The histograms along the top and right margins show the single-axis distributions. The choice probability distribution shows a mean value across all observations near 0.55. The response ratio distribution reveals that the average firing rate change that produced the observed choice probability values. On average, cells in MT fired about 7% more on preferred direction choice trials. The jagged curve shows the running mean of 41 adjacent observations. Over the central core of the data distributions, this mean is approximately linear. Two sharp breaks in the average choice probability occur near response ratios of about 0.7:1 and 1.5:1; outside this range, choice probabilities show no reliable dependence on response ratio. These breaks occur at choice probability values of about 0.3 and 0.75, suggesting that values of choice probability more extreme than these arise largely by chance.

The analyses shown in Figs. 3A and 3B suggest that it is legitimate to pool choice probabilities across stimulus coherence levels. We scaled each observed firing rate by the mean and standard deviation for that stimulus condition (z transform). This scaling has no effect on the rank order of individual observations, and the choice probability for each condition is therefore unaffected. However, it allowed us to combine spike counts from all coherence levels into a single pair of distributions, from which we could then calculate a single choice probability for each neuron. Using this method, we derived choice probabilities for the preferred, null, and zero coherence stimulus conditions for each of the 299 MT cells. The distributions of these values are shown in Fig. 5.

We devised a permutation test (Efron & Tibshirani, 1993) to assess the significance of the deviation of each observation from chance (0.5). We randomly permuted the data for each trial so that the association of neuronal and behavioral response was abolished, while leaving the distributions of neuronal response and behavioral judgment untouched. We calculated the distribution of choice probabilities expected in the absence of this association from 2000 such permutations. We took observed choice probability values that lay outside the central 95% of the distribution to be significant. Cells with significant values are shown as stippled bars in the histograms in Fig. 5. It is evident that relatively few cells had pooled choice probability values that achieved statistical significance when examined in isolation (85/296, 29%, for the preferred direction, 70/287, 25%, for zero coherence, and 74/293, 25%, for the null direction). Of those cases that did achieve significance, however, the great majority (195/229, 84%) had choice probabilities greater than 0.5, meaning that they had a significant *positive* association with the monkey's behavioral choices. Of the 876 choice probabilities in these three distributions, only 36 (4%) had values significantly below 0.5.

We also extended our z-transform method to combine choice probabilities across both stimulus conditions and neurons for our entire sample, to calculate a "grand" choice probability reflecting the strength of the association for the entire pool of neurons for each condition. We scaled the response for each condition by its mean and standard deviation, and then pooled all of the resulting response distributions. We used the permutation test described above to evaluate the significance of the deviation of each "grand" choice probability from chance. To compare two "grand" choice probabilities with each other, we devised a second permutation test. We formulated the comparison as a test of the hypothesis that the observed difference between two choice probabilities could arise by chance, if both sets of observations were sampled from the same parent distribution. We took the union of the two sets of z-transformed

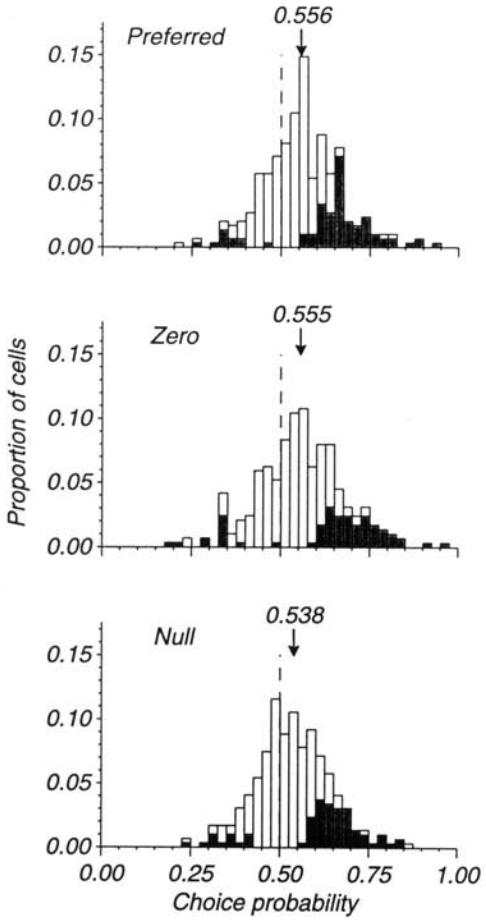

Fig. 5. Distributions of neuronal choice probability for all 299 cells in the sample, compiled separately for preferred direction (296 cases; a few lacked sufficient trials for analysis), null direction (293 cases), and zero coherence (287 cases) responses. Stippled bars indicate cases that were significantly different from 0.5 by the permutation test described in the text.

responses to form a single joint distribution, retaining the association between response and decision. We randomly sampled this joint distribution to form two sets of values, each with the same number of observations as the test distributions, and calculated the difference in choice probability between them. We estimated the distribution of such differences by repeating this 2000 times, and took difference values that lay outside the central 95% of the distribution as significant.

For the remainder of the paper, we will use statistics based on these permutation techniques to test the significance of choice probability values. These statistics are based in an unbiased way on the data themselves, and do not embody assumptions about sample sizes and distributions that are implicit in more conventional tests. In no case did the permutation statistic lead to a conclusion that contradicted the outcome of a conventional distributional test. The "grand" choice probabilities calculated in this way for the three distributions in Fig. 4 are 0.557, 0.553, and 0.534, respectively; these values are based on over 37,000 trials for the preferred and null stimulus directions, and over 20,000 trials for the zero-coherence trials. All three values were significantly different from 0.5 ($P < 0.0005$ in all cases), and the null direction value was significantly lower than the other two ($P < 0.0005$). The values for the preferred direction and zero coherence did not differ from one another (permutation test, $P = 0.399$).

Reliability of the choice probability measure

To interpret the distributions shown in Fig. 5, it is important to have some sense of the reliability of the individual observations from which the distributions were formed. We approached the question of reliability and repeatability empirically, by subdividing the data for each cell into two sets, using even-numbered trials for one set and odd-numbered trials for the other; we then separately calculated the choice probability for each subset.

The results of this comparison are shown in Fig. 6, in which the different estimates are plotted as a function of the number of trials used for the calculations of choice probability. Each vertical line connects the two values of choice probability obtained from the divided data set for a single cell. The jagged curve shows the running mean of 21 adjacent observations. We draw several conclusions from this analysis. First, as would be expected, the consistency of the estimate of choice probability improved in an orderly way with the number of trials that contributed to the measurement, as is evident from the prevalence of short lines to the right of the plot and long lines to the left. Second, the central tendency of the value of choice probability was not affected by the number of trials contributing to the measurement, as is evident from the lack of a consistent trend in the running mean. Third, most values of choice probability larger than about 0.7–0.8 arise largely by chance; they are only seen near the left end of this graph, where the values are less reliable. This reinforces the similar conclusion we drew from Fig. 4. Finally, the highly reliable points near the right end of this plot reveal that individual cells can have choice probabili-

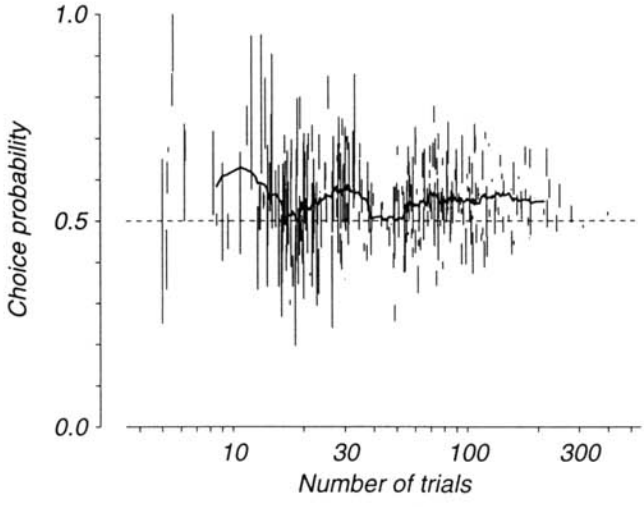

Fig. 6. Repeated-measure reliability of the choice probability for 294 of the 299 neurons (five neurons were omitted because of an insufficient number of trials). Each vertical line connects two values of the estimated choice probability for each neuron, calculated separately for even and odd numbered trials. The solid line through the center of the graph plots the running average of 21 adjacent observations, ordered by number of trials. Four types of trial are used for each calculation (preferred and null direction decisions for each subset of trials), and the values on the abscissa correspond to the average number of entries for these trial types.

ties that differ both from one another and from the population mean.

A second way to visualize individual cells' data is shown in Fig. 7, in which the two repeated values of choice probability are plotted against one another. Cells whose values were significant on even trials are plotted as plus signs, cells whose values were significant on odd trials are plotted as crosses, cells whose values were significant on both subset analyses are plotted as stars (superimposed plus signs and crosses), and cells whose values were significant on neither subset are plotted as small dots. The sensitivity of the permutation statistic is revealed by the point at which significant cells appear on either axis; naturally this sensitivity will depend on N. While there is substantial scatter of these data about the diagonal, it is plain that there was a general tendency for cells to have similar values in the two subset analyses. The prevalence of doubly significant cells in the top right quadrant (asterisks) is further evidence of the overall repeatability of the measure. Overall, the correlation between the two values of choice probability was 0.505, which was highly significant ($F = 99.7$, $df = 1,292$, $P < 0.0001$). There was no difference on average between the choice probabilities measured on even and odd trials (permutation test, $P = 0.260$). The magnitude of the covariance in this plot also reveals, like Fig. 6, that individual cells can have reliably different choice probabilities. We will return later to the question of whether the cells having higher choice probabilities differ in other ways from their less well-associated companions.

Stimulus effects

The analysis in the preceding section reveals that for our population of neurons, choice probability departed from the value of 0.5 expected by chance. We conclude that there is a systematic relationship between the firing rates of MT neurons and the decisions made by the monkey on single psychophysical trials. The most interesting interpretation of this observation is that these neuronal signals contribute directly to the decisions made by the monkey, and that variation in the signals causes variation in the monkey's behavior. Such a causal relationship should be influenced by changes in the visual stimulus, and in this section we explore the effects of several different stimulus manipulations designed to clarify the relationship between neuronal activity and behavioral choice.

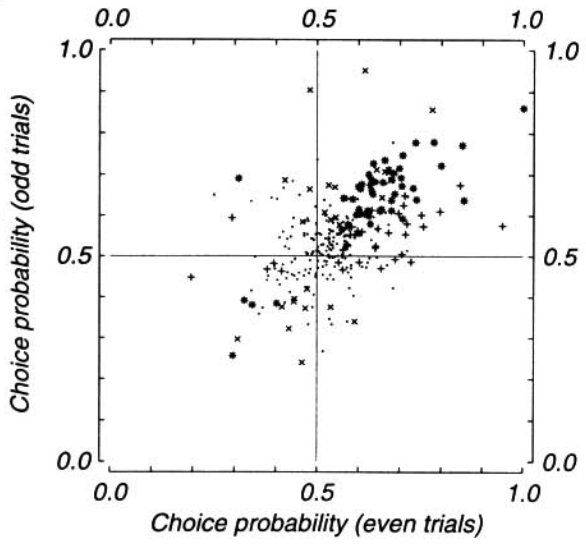

Fig. 7. Comparison of choice probability calculated from the odd and even trial subsets used in Fig. 6. Values that differed significantly from chance by the permutation test on the even subset are shown by +, on the odd subset by ×, on both subsets by *, and on neither by a point.

Trial-by-trial stimulus variation

We designed the first such manipulation to explore the possibility that the source of our effect was trial-by-trial variation in the stimulus itself. Stimuli of a given direction and coherence normally differed from trial to trial in the exact placement of dots in space and time, and consequently in the precise motion signal presented. Some trials by chance included more preferred direction motion, and on such trials one would expect an increased response from the neuron and also an increased proportion of preferred direction judgments; other trials included less preferred direction motion, which should lead to the reverse outcome. This effect, were it significant, could produce the phenomenon that we are describing. To control for this possibility, in some experiments we presented stimuli without this random variation. That is, for each set of stimulus parameters, precisely identical dot patterns were presented on every trial. We asked whether the choice probabilities were affected by the stimulus variation. We performed this control in two ways.

First, we collected data from 43 cells in monkeys J and W without trial-to-trial stimulus variation. We compared the magnitude of their choice probabilities with those of 108 cells from the same two monkeys in which stimulus variation was present. Fig. 8A shows the distributions of choice probability for these two groups of cells. The upper panel shows the distribution of choice probabilities measured with trial-to-trial stimulus variation; the lower panel shows the distribution measured with the same stimulus presented every trial. The two sets of values are quite similar, and each deviates significantly from chance (permutation test, $P < 0.0005$ in both cases); the values are relatively low because of differences between animals, which we consider below. The values do not differ significantly from each other (permutation test, $P = 0.5495$), suggesting that removing stimulus variation did not discernibly affect the choice probability. To probe this issue more directly, we compared the two stimulus conditions in the same neurons. We measured the choice probabilities under both conditions in an additional group of 24 cells from monkey E. These measurements were made only at 0% stimulus coherence, and trials of each type were randomly interleaved. Fig. 8B shows the results of this experiment, in the same format as Fig. 8A. There was no significant difference between the choice probabilities under the two conditions (permutation test, $P = 0.68$), and the mean of each distribution was significantly different from 0.5 (permutation test, $P < 0.0005$). The two measurements of the choice probability for each neuron were significantly correlated ($r = 0.452$, $F = 5.6$, $df = 1,22$, $P = 0.027$). We conclude that choice probability was not strongly influenced by stochastic variation in the stimulus. This is consistent with our earlier finding that this form of stimulus variation has no detectable effect on the trial-by-trial variance in cell discharge rate (Britten et al., 1993). Our interpretation is simply that the effect of trial-by-trial stimulus variation is negligible compared to other factors that contribute to the covariation of neuronal response and behavioral judgment.

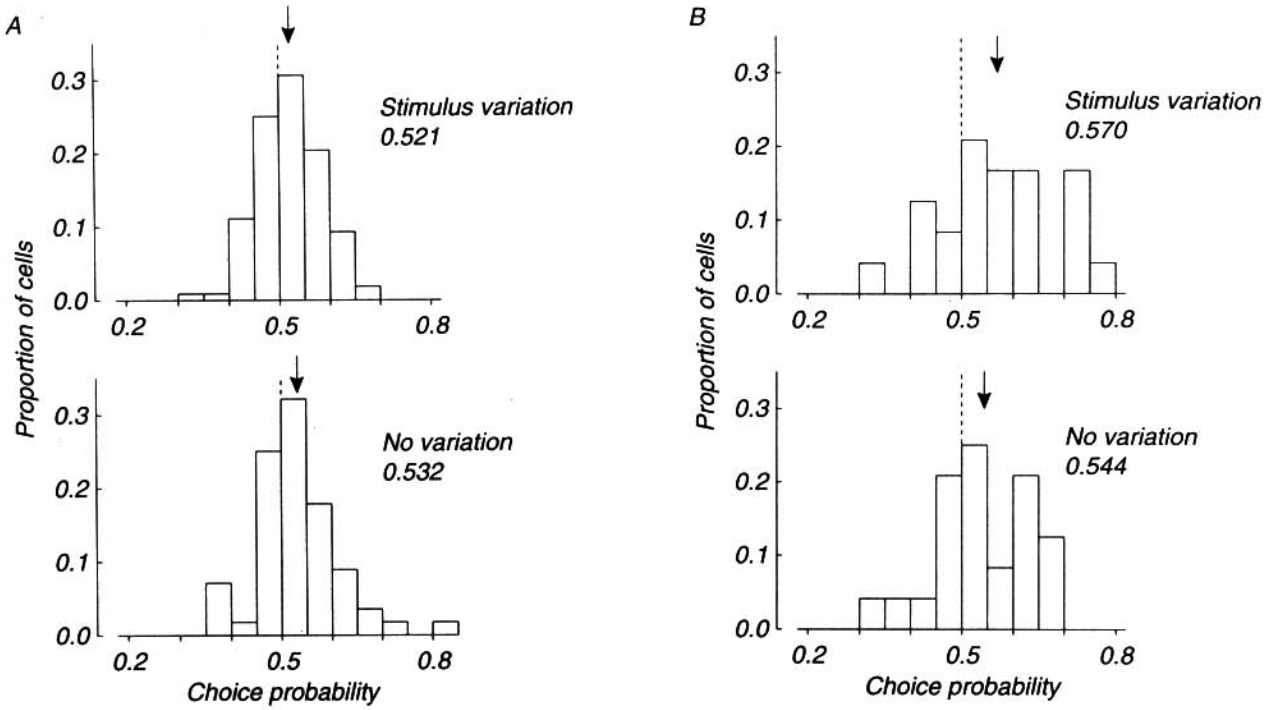

Fig. 8. Dependence of choice probability on the presence of trial-to-trial variance in the stimulus. A: Distributions of choice probability for 108 cells from monkeys W and J studied with stimulus variation (upper histogram) compared with that for 43 different cells from the same monkeys studied with no variation (lower histogram). B: Choice probability distributions for 24 cells from monkey E for which we made interleaved measurements with both types of stimulus. Both measurements were made with 0% coherence stimuli which were randomly interleaved within blocks of trials that also contained stimuli with non-zero coherence.

Matching task demands to neuronal stimulus preferences

Having established that choice probability is not determined by short-term stimulus fluctuations, we now turn to the relationship between choice probability and the "informativeness" of the neuron under study. Recall that in our experiments, visual stimuli were carefully optimized for each neuron. Under these conditions, an interpretation of choice probabilities greater than chance is that the neuron under study contributes to the monkey's judgments. Therefore, modifying the stimulus conditions to make the neuron's discharge *uninformative* for a particular discrimination should reduce the choice probability to chance. We explored this using two different stimulus manipulations to render the cells' signals less directional. In one experiment, we removed the stimulus from the receptive field of the neuron, but otherwise left its parameters unchanged (i.e. we used the same size, speed, and directions of movement). In a second experiment, we rotated the axis along which the monkey made his decision while the stimulus remained located in the neuron's receptive field.

To study the effect of stimulus placement, we altered the position of the stimulus relative to the receptive field by changing the location of the fixation point, which we placed either so that the receptive field was centered on the stimulus, or so that its border lay at least half a receptive-field diameter from the nearest edge of the stimulus. The fixation point was placed so that the eccentricity of the stimulus was approximately the same in each set of trials, and so that the target LEDs were roughly equidistant from fixation for each condition. On- and off-receptive field trials were interleaved. Fig. 9 illustrates the

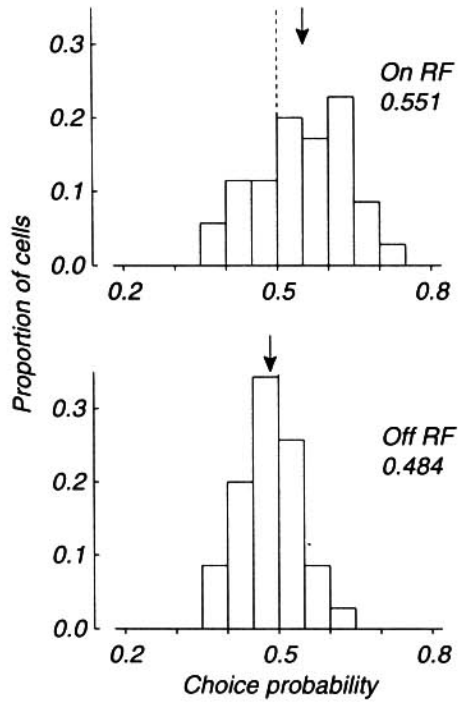

Fig. 9. Dependence of choice probability on the location of the stimulus. The choice probability for each of these 33 cells was measured in two ways: with the visual stimulus either on (upper histogram) or off (lower histogram) the cells' receptive fields, as described in the text. All other stimulus parameters remained the same.

effect of removing the stimulus from the receptive field, for 33 cells recorded from monkey E. The choice probabilities for the on-receptive field condition were significantly greater than chance (permutation test, $P < 0.0005$), and also systematically larger than those for the off-receptive field condition (permutation test, $P < 0.0005$); the choice probabilities for the off-receptive field conditions were slightly but significantly *lower* than 0.5 (that is, they were inversely related to the monkey's decision), a result that might be related to the modulation of MT neuron responses by regions outside the conventional receptive field (Allman et al., 1985). We conclude that the relationship between firing rate and decision was abolished (and perhaps reversed) by moving the stimulus off the receptive field of the cell.

The reduction of the choice probability resulting from removing the stimulus from the receptive field of the cell might be a simple consequence of the reduced firing rates that this manipulation produced, and we wished to exclude this artifactual explanation. Recall that in Fig. 3B, we examined the relationship between choice probability and neuronal firing rate. There was a weak relationship between choice probability and neuronal firing rate, evident for very low firing rates (<0.5 impulses/s). Among the off-receptive field data, such low rates were observed in three of 33 experiments, and removing these three cells did not affect the outcome of the analysis.

A more subtle way to modulate the information carried by MT neurons is to leave the stimulus centered on the receptive field, but to alter the axis of movement so it was roughly orthogonal to the original, optimal axis. This reduced the directionality of the cells, but because of their broad directional tuning it did not in general abolish visual responses altogether. It also proved very difficult to eliminate directionality completely, since the flanks of the direction tuning function are often asymmetric, and a few degrees of error from the perfect "balance point" could produce substantial directional responses. Since in general this manipulation did not abolish visually evoked activity, we were able to assign the "preferred" direction in these cases simply by choosing the direction eliciting the larger response. In this experiment the two sets of trials were presented in blocks. We performed this experiment on 45 cells from monkeys E and J, and the results are shown in Fig. 10. The permutation technique shows that the values of choice probability for both stimulus conditions were significantly greater than 0.5 ($P < 0.0005$), but also that the choice probability was significantly lower for the orthogonal condition ($P < 0.0005$) than for the on-axis condition. Thus, the relationship between neuronal firing and behavioral choice was attenuated but not abolished by this manipulation, which attenuated but did not abolish visually elicited responses.

Both the off-receptive field and off-axis experiments allow the interpretation that significant choice probabilities were evident when the visual stimulus being discriminated was appropriate to activate the neuron being recorded. If the neuron's signals were irrelevant to the behavioral judgment, then the value of choice probability fell to values near chance.

Time course of the choice probability signal

In principle, the decision-related activity we have described could arise because the monkey's decisions depended on the activity of the neuron being recorded, or because the neuron being recorded was influenced by the monkey's decision. We explored

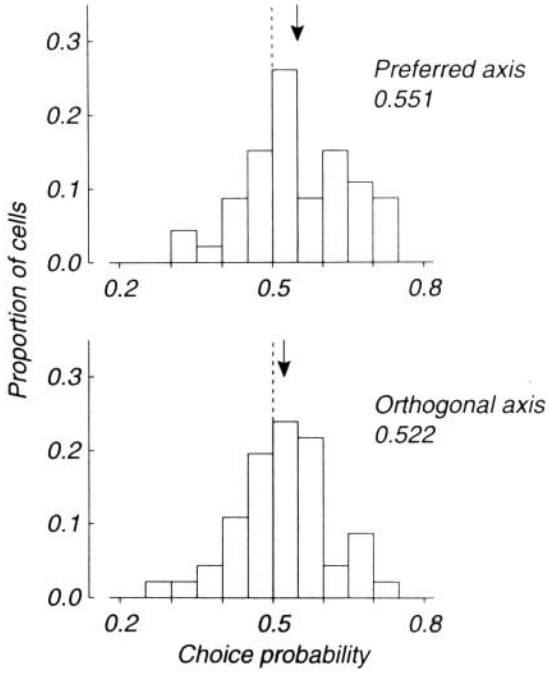

Fig. 10. Dependence of choice probability on the axis of motion of the stimulus. The choice probability for each of these 45 cells was measured in two ways: with the visual stimulus moving along the neuron's preferred axis (upper histogram), or roughly orthogonal to it (lower histogram).

the direction of causality by examining the time course of the firing rate differences that we observed. We have until this point described only an integral measure, incorporating with equal weight all spikes recorded during the 2-s stimulus period. To explore the dynamics of the relationship, we examined how firing rate changed with time ***within*** the stimulus period. If the choice probability were related to feedback from the decision that the monkey made, we would expect the firing rate difference between "preferred-decision" and "null-decision" trials to be delayed until the perceptual judgment became more reliable; in an average record the difference would evolve gradually during the stimulus period. If, on the other hand, it were the neuronal response that influenced the perceptual decision, we would expect all spikes to be counted more or less equally, and the effect to emerge early and be more or less stationary throughout the response. To study this question, we averaged the normalized response histograms for the 75 cells in the sample that showed a significant positive choice probability (>0.5 only). We averaged only the responses to 0% coherence stimuli, to avoid contamination by the dynamics of the directional signal itself. Beginning 300 ms before the onset of the stimulus, we made separate averaged rate records for preferred decision and null decision trials, both normalized to the peak of the preferred decision histogram. The two histograms are superimposed and plotted in Fig. 11A, and the difference between them is plotted in Fig. 11B. This analysis reveals that the difference in firing rates emerged very early in the response—within approximately 50 ms—and remained constant for the duration of the stimulus. We take this as evidence that significant choice probabilities arise not because of feedback from the decision itself, but because signals from MT neurons are likely to feed forward into the deci-

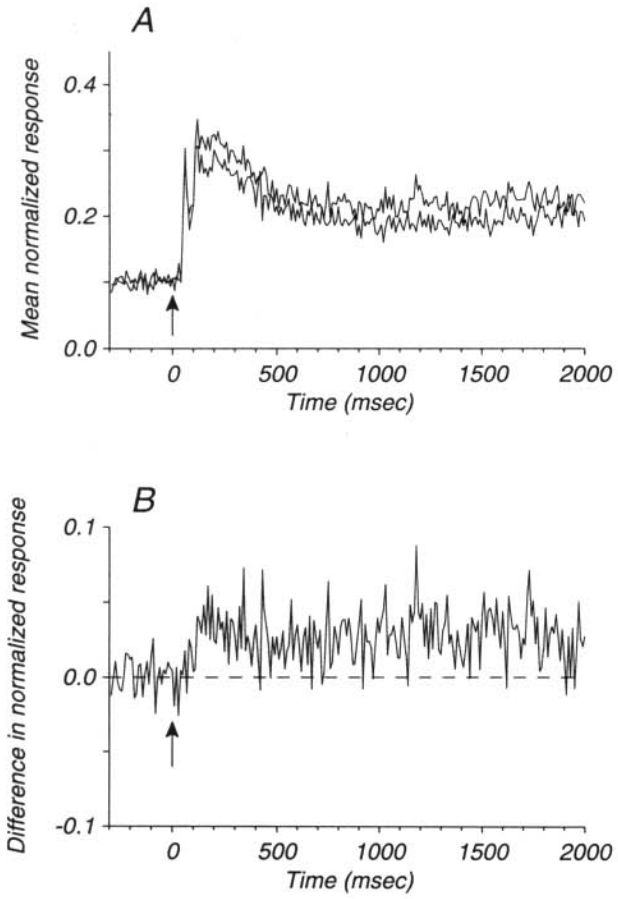

Fig. 11. Time course of the firing rate difference that underlies the choice probabilities. The 0% coherence responses of 75 cells that showed a significant choice probability were combined. Each cell gave a pair of averaged response histograms (bin width: 10 ms) corresponding to preferred and null direction decision trials. Each pair was normalized to the peak of the preferred direction histogram. A: Pooled average response histograms for each response direction, with the upper representing the preferred direction decision trials and the lower showing the null direction decision trials. B: The difference between the two responses as a function of time. Note that the response difference is only present during the visual stimulus period, and not during the fixation period prior to stimulus onset (arrows).

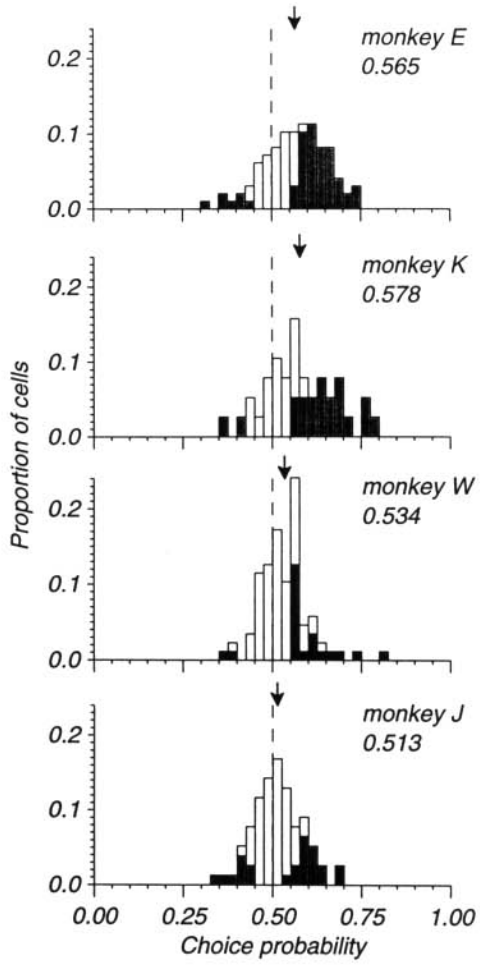

Fig. 12. Choice probability distributions from the four monkeys (monkey E: 97 cells; monkey K: 38 cells; monkey W: 87 cells; and monkey J: 77 cells). The choice probabilities were pooled for all stimulus conditions. The stippled bars, as in Fig. 5, indicate neurons whose choice probabilities differed significantly from 0.5 on the permutation test.

sion process. Furthermore, the absence of a rate difference in the fixation period before stimulus onset suggests that any effects of response bias or selective attention which might be evident before the stimulus are not the source of the choice probabilities we observed.

Interanimal differences

Our monkeys differed from each other in their psychophysical performance and in the sensitivity of their individual neurons (Britten et al., 1992). We were therefore interested to notice that choice probability also differed among animals. Fig. 12 shows the distributions of the neuronal choice probabilities individually for each animal. The distributions are different for each animal, and those for monkey E and monkey K are shifted to the right with respect to the other two. These two animals each had relatively large numbers of significant choice probability values (more than half the cells in each case), the great majority of which were greater than 0.5. The mean of the distribution for each monkey was significantly greater than 0.5 (permutation test, $P < 0.0005$ for monkeys E, W, and K, $P = 0.03$ for monkey J). Although the value for monkey J was only barely significant, substantially more cells than expected showed a significant choice probability in this monkey (24/77, 31%, stippled bars); two-thirds of these values were greater than 0.5. It is worth noting in this context that monkey J differed from the other monkeys in having higher psychophysical and neuronal thresholds (Britten et al., 1992). Considering all animals, however, we did not find any simple relationship between neuronal choice probabilities and either psychophysical or average neuronal sensitivity.

Since the two monkeys with the largest average choice probabilities (E and K) were also the last to be studied, we wondered whether the apparent differences between monkeys actually reflected differences due to some unknown factor (such as changes in experimental procedure) that occurred with time. An analysis of covariance revealed, however, that neuronal choice probability varied significantly with monkey ($F = 6.6$, $df =$

3,296; $P = 0.0004$), but not with the date of recording ($F = 0.19$, $df = 1,298$, $P = 0.66$).

Relationship of choice probability to neuronal threshold

If we consider the choice probabilities to reflect the contribution of individual cells to the monkey's psychophysical judgment, then some cells might be more strongly associated with the decision than others. Naturally, we wondered whether the neurons with the highest sensitivities (which carried the "best" sensory signals) had higher choice probabilities than those with lower sensitivity. Sensitivity of a neuron may be measured in many ways, but in previous work we have used a method derived from signal detection theory to calculate a *coherence threshold* for each cell, the coherence level at which the neuron achieved a criterion level of directionality (see figure legend and Britten et al., 1992 for more detail). The relationship between choice probability and neuronal threshold is shown in Fig. 13. The correlation between these measures was −0.328, and was highly significant ($r = -0.328$, $F = 35.5$, $df = 1,295$, $P < 0.0001$). The plot also shows the best linear relationship derived from a maximum-likelihood regression analysis.

Each monkey's data are drawn with different symbols, and inspection reveals that individual animals differed substantially from one another. The two monkeys with the lowest average choice probabilities (monkeys J and W) are illustrated with open symbols, and for these monkeys, the relationship between choice probability and threshold was not significant ($r = -0.074$, $F = 0.89$, $df = 1,162$, $P = 0.35$). For the other two monkeys, E and K, the relationship was strong ($r = -0.562$, $F = 60.6$, $df = 1,131$, $p < 0.0001$). This relationship suggests that neurons with lower thresholds are more closely associated with the monkeys' decisions.

Discussion

We have previously documented the exquisite motion sensitivity of neurons in extrastriate area MT by studying the relationship between their responses and the direction and strength of visual motion signals delivered to their receptive fields (Britten et al., 1992). These results suggested that MT neurons might provide the signals supporting behavioral choice in visual motion discrimination tasks. To approach this question from another direction, we have now shown that signals carried by a single MT neurons are associated, trial by trial, with the monkeys' decisions. On a given trial, the monkey was more likely to make a decision in favor of the preferred direction of a neuron when the neuron was firing more vigorously. The magnitude of this association between neural response and behavioral choice was modest, but given the large number of neurons in MT (as well as in other areas), it is remarkable that such a correspondence exists at all.

Choice probability as a measure

We describe the relationship we have uncovered with a measure we term *choice probability*, a distribution-free metric closely related to the ROC analysis of signal detection theory (Green & Swets, 1966). We were, in fact, initially drawn to this approach because of its conceptual tie to signal detection theory. In contrast to traditional uses of signal detection theory, however, we do not seek a relationship between the *stimulus* and neuronal response; instead we use it to detect a relationship between neuronal activity and the monkey's *choice*.

The measurement of choice probability proved to be more difficult than the other kinds of neuronal response measurements that we have undertaken in this set of studies. As is graphically shown in Fig. 6, choice probability is a subtle quantity, not well estimated from small numbers of trials. The dependence of the reliability of the estimate of choice probability on trial number is roughly as one would expect, but the estimate does not become reliable until each choice distribution contains roughly 100 trials. It is also important to realize that for these trials the stimuli must be near threshold so that the monkey makes a useful number of errors on the psychophysical task.

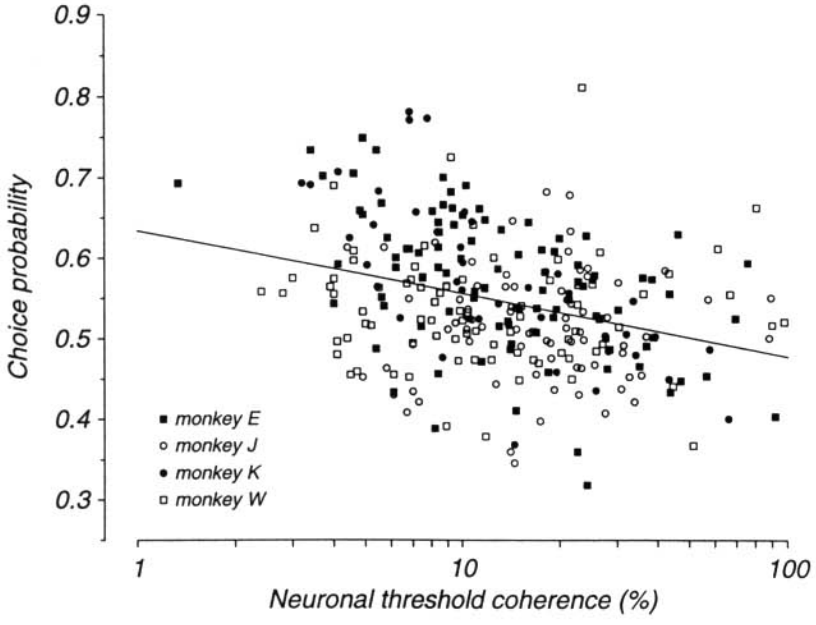

Fig. 13. Relationship between choice probability and neuronal threshold. The neuronal threshold was derived from an analysis presented elsewhere (Britten et al., 1992); it corresponds to the lowest stimulus coherence at which the neuron's response could be used to distinguish preferred from null direction motion on 82% of trials. The relationship portrayed here differed considerably across monkeys; the two animals with the highest average choice probability (E and K) were the only ones to show a significant relationship individually. These two animals' data are drawn with solid symbols. Choice probabilities were derived from all stimulus conditions combined; similar effects were observed when choice probabilities for different directions of motion were compared separately.

As a result, our experiments barely sufficed to uncover the choice probability effect that is the subject of this paper.

Consider, for example, the significance of an individual neuron's choice probability. The average deviation from chance of the choice probability effect is about 0.05; this is smaller than the expected dispersion of the estimate for the number of trials we obtained for most cells. Therefore, tests of the significance of *individual observations* reveal significant effects only for about 25% of cells (cf. Figs. 5 and 11); we rely upon combined measures for our strongest conclusions. One defensible interpretation of this is that individual neurons do not in fact have reliable choice probability values – perhaps only the population of neurons as a whole should be considered to have a reliable association with response. In fact, we believe that individual neurons *do* differ in their choice probabilities. For example, neurons that have high sensitivity (low thresholds) tend also to have high values of choice probability (Fig. 13).

Related observations

The approach of simultaneously recording neuronal activity and psychophysical choices near threshold is not new, although it is rather rarely used. Logothetis and Schall measured activity in MT simultaneously with directional decisions under uncertainty conditions resulting from binocular rivalry (Logothetis & Schall, 1989), and some of their cells showed results qualitatively similar to ours. Curiously, though, they found approximately equal numbers of cells with positive and negative association to the behavioral report. As noted above, Celebrini and Newsome (Celebrini & Newsome, 1994) have used this method in recordings from area MST. Related observations have also been made in the somatosensory system. Vallbo and Johannson (Vallbo & Johannson, 1976) reported a similar effect in recordings from cutaneous mechanoreceptor afferents. Dubner and his colleagues have recorded in both the medullary dorsal horn and in S1 while monkeys were detecting temperature increments near threshold (Dubner et al., 1989; see also Mountcastle et al., 1990; Sinclair & Burton, 1991 for related observations in another somatosensory context). These studies report choice-response associations qualitatively similar those we have described, although the nature of somatosensory experiments makes it difficult to rule out explanations related to other aspects of the animal's behavior. For example, the animal can change the way it touches the discriminanda from trial to trial, and thus the exact magnitude of the stimulus. In fact, Sinclair and Burton conclude that this was the principal cause of the correlation they observed.

Mechanism

Plainly, we lean to the view that the choice probability effect is a statistical signature of the contribution that neurons in MT make to perceptual judgments. Before we can assert this view with confidence, however, we must consider a variety of other, less interesting, explanations.

The simplest possible explanation for the relationship we observed is that it reflects the inherent trial-to-trial variability present in the stimulus itself. As a control for this, we presented stimuli which were identical for any particular direction and coherence. In these cases, the choice probability remained significant, and was as large as it was in the presence of stimulus variation (Fig. 8). Our results are consistent with the idea that a component of the choice probability could be due to stimulus variation, but it is only a small part of the effect that can be explained in this way.

Eye movements are always a concern in interpreting data from experiments in alert monkeys. In the present experiments, eye movements were restricted by the computer (which aborted trials with excessive eye movement), and monitored nearly continuously by the experimenter. It remains possible that the small residual eye movements could modestly influence the firing rates of the neurons we recorded. However, for eye movements to produce the choice probabilities we observe, these would not only have to modulate neuronal discharge, but would have to do so in a manner that was correlated with the animal's subsequent choice. The most plausible possibility is that the monkey might within very narrow permitted limits attempt to track the seen motion. But since such tracking would reduce retinal target speed and therefore reduce the neuronal response (Newsome et al., 1988), the effect would be to decrease rather than increase the measured choice probability.

Significant choice probabilities could also arise if linked changes in neuronal and behavioral sensitivity occurred over the course of an experiment; just such an effect was indeed reported by Zohary et al. (1994), who showed that during an experimental session, both neuronal thresholds and behavioral performance tended to improve. The portion of the choice probability deviation from chance that can be due to this effect is, however, not large (less than 0.005); this effect can also plainly not be a factor for stimuli of 0% coherence. We performed a smoothing analysis to remove long-term trends in the data that could affect the calculation of choice probability; this analysis confirmed that the effect of these long-term trends was negligible.

Finally, we considered the possibility that global modulations of attention or arousal state might jointly affect both neuronal and behavioral sensitivity, artifactually creating a significant choice probability. This could result, for example, if the monkey made correct choices more often on trials with heightened attention and if the neuron were simply more sensitive (i.e. more directional) on such trials (e.g. Moran & Desimone, 1985). Note that this mechanism could lead to a choice probability for any directional neuron, whether or not it contributed to the monkey's perceptual judgments. This could not, however, explain the existence of a choice probability for trials on which the motion stimulus had 0% coherence. While neuronal activity might conceivably be modulated by attention on such trials, there is no basis for supposing that the monkey could make more "correct choices" on these trials, since "correct" choices are arbitrary at 0% coherence. On these trials, then, the monkey's decisions would be randomly associated with trial-to-trial fluctuations in neuronal responsiveness unless the observed neuronal variability actually influenced the monkey's choices; Fig. 5 shows instead that choice probability was just as strong for 0% coherence as it was for other stimuli. Moreover, we have presented evidence elsewhere that attention has no discernible effect on the thresholds of MT neurons (Britten et al., 1992). The final evidence against such "global" explanations comes from experiments performed in the current study using ineffective or suboptimal visual stimuli (Figs. 9 and 10). Recall that when the activity of a neuron was less relevant to the discrimination being performed, the choice probability was reduced or eliminated.

Thus, under the conditions we have tested, choice probability is not ubiquitous, but is more robust in the specific subset of neurons that provides *information* relevant to the present task. Our interpretation is that signals from this subset of neurons are being used to form the behavioral choice.

Conclusions

We believe that finding a significant choice probability for a given pool of neurons provides good evidence for the involvement of the pool in perceptual judgments. We have in other experimental and theoretical work devoted substantial effort to trying to establish the size and nature of the neuron pools supporting perceptual choice (Britten et al., 1992; Shadlen et al., 1995). Data concerning neuronal thresholds to visual stimulation do not by themselves provide an adequate constraint for such modeling—they are consistent with several very different notions of how "relevant" neuronal signals are selected and pooled (Britten et al., 1992). Our choice probability data provide decisive additional constraints.

The first important constraint is due to the fact that choice probabilities were roughly equal for stimuli moving in the preferred and null directions, as well as for stimuli without net motion (Fig. 5). This suggests that signals from relevant MT neurons are *always* monitored when they can be informative, even when the stimulus moves opposite to the neuron's preferred direction. Thus, we conceive of perceptual decisions being derived from the comparison of activity in separate pools of MT neurons preferring different directions, rather than from particular neurons that are very active because the stimuli precisely match their preferences. The difference between the choice probabilities in the two directions (Fig. 3A) may provide information about the balance of these pools.

A second constraint is due to the relatively low values of choice probability we observed for individual neurons. These values are not consistent with models in which perceptual judgments are based on very small numbers of neurons, because these models would predict a much higher degree of association between the relevant neurons and the behavioral judgments. We have therefore modeled the way that pools of neurons could contribute to perceptual judgment, an exercise that we will describe in detail elsewhere (Shadlen et al., 1995).

Our analysis provides physiologists with a new way to probe the contribution of particular neurons to perception and action. The traditions of sensory neuroscience rely heavily on the indirect inference of a functional role for a group of neurons simply because they possess a particular response property. Yet sensory signals in the brain serve many functions, and it is presumptuous to imagine that a particular neuron has a particular role because we as physiologists tested its responses in a particular way and found it adequate. The measurement of choice probability offers a powerfully different perspective on this crucial question, and its presence allows us to make a principled argument for the involvement of neuronal activity in behavior.

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