

Neural population code for fine perceptual decisions in area MT

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In the middle temporal (MT) area of primates, many motion-sensitive neurons with a wide range of preferred directions respond to a stimulus moving in a single direction. These neurons are involved in direction perception, but it is not clear how perceptual decisions are related to the population response. We recorded the activities of MT neurons in rhesus monkeys while they discriminated closely related directions, and examined the relationship between the activities of neurons tuned to different directions and the monkeys' choices. Perceptual decisions were significantly correlated with the activities of the highest-precision neurons but not with those of the lowest-precision neurons. The combined performance of the high-precision neurons matched the monkeys' behavior, whereas the ability to predict behavior based on the entire active population was poor. These results suggest that fine discrimination decisions are crucially dependent on the activities of the most informative neurons.

Do all neurons activated by a stimulus contribute to its perception or is it just a specialized subgroup that does so? This fundamental, yet difficult question underlies attempts to explain how perception emerges from neural activities^{1–4}. We measured the activities of a distributed population of visual neurons in monkeys (*Macaca mulatta*) making perceptual decisions to determine which parts of the neural population response are related to the decisions.

In many parts of the cortex, a large population of neurons responds to a single stimulus. Understanding which part of this population response underlies perception has been a longstanding problem. Population-coding schemes propose that all active neurons contribute to perception, to a greater or lesser extent^{4,5}. In contrast, the lower-envelope principle asserts that perceptual decisions are solely determined by the most sensitive neurons and are little influenced by the large number of other, less-sensitive, neurons^{2,6}. Indeed, single neurons are sensitive and reliable detectors of stimuli^{2,6–10}. Some studies have even linked the activities of single neurons to perceptual decisions¹⁰. For example, in area MT, a stimulus moving in a single direction typically activates many neurons with a broad range of preferred directions^{11–16}. The activity of the subset of MT neurons whose preferred direction is the same as the stimulus direction^{17–20} is related to perceptual decisions on a trial-by-trial basis¹⁹. However, these studies did not report the population response from neurons whose preferred directions were different from the stimulus direction. Another study reported the entire population response but not the perceptual decisions²¹. Therefore it is unknown whether a population-coding scheme or the lower-envelope principle best describes the relationship between MT neural activity and perception.

We trained two monkeys on a fine direction-discrimination task and measured the activities of neurons tuned to various directions while the monkeys performed this task. We computed the relative contribu-

tion made by each neuron in the population to the monkeys' decisions using two different measures of correlation between the neural activities and decisions. These measures showed that for a given stimulus direction, the activities of neurons with the highest precision were significantly correlated with the monkeys' decisions on a trial-by-trial basis, whereas the activities of neurons with the lowest precision were not. Analysis of various neural coding schemes showed that only those schemes that selectively emphasize the activities of the high-precision neurons could account for the psychophysical precision. Broad uniform pooling of all active neurons yielded a precision three times lower than the psychophysical performance.

RESULTS

Psychophysical performance

In the fine direction-discrimination task (**Fig. 1a**), a reference stimulus moving upward was presented for 1 s. After a 0.5–1 s interval, a test stimulus moving in a direction either clockwise or counter-clockwise from the reference direction was presented for 1 s. Both reference and test stimuli were random dot kinematograms (Methods). Monkeys indicated whether they perceived the test direction to be clockwise or counter-clockwise from the reference direction by making an eye movement to one of two target dots that appeared after the test stimulus disappeared. The direction difference between reference and test stimuli was varied from -3° (counter-clockwise) to $+3^\circ$ (clockwise). Psychometric functions quantified the monkeys' performance (**Fig. 1b**). The average threshold for both monkeys over all the sessions was 1.7° . Best human thresholds^{22–24} are about $1–2^\circ$, indicating that the monkeys were adept at the task.

Neural precision for fine discrimination

We recorded the responses of 240 MT neurons while monkeys L ($n = 192$) and M ($n = 48$) performed this task (Methods). We quantified the

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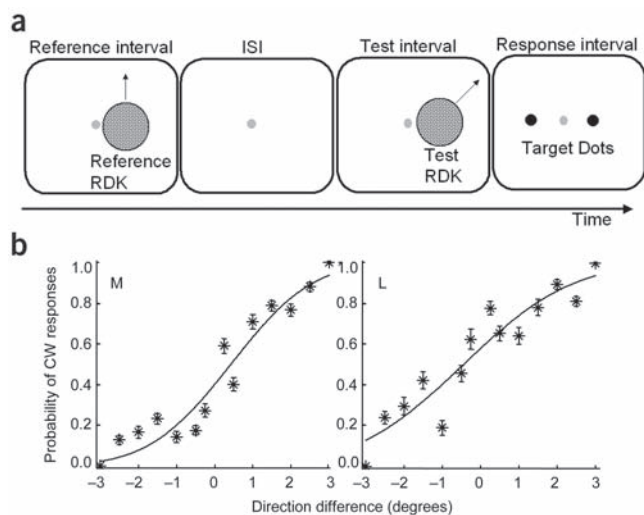


Figure 1 Fine direction-discrimination task and the monkeys' psychophysical performance. **(a)** The task consisted of four intervals. The monkey held fixation on the central dot for 500 ms before the reference stimulus was presented. The reference stimulus, a random dot kinematogram that moved up, was presented for 1 s. This was followed by an interstimulus interval (ISI) of 0.5–1 s, during which there was no stimulus and the monkey continued to fixate on the central dot. A test stimulus, whose direction was either clockwise or counter-clockwise from the reference (shown exaggerated), was presented for 1 s. Then, 250 ms after the test stimulus, two target dots were displayed, and the monkey broke fixation to indicate the perceived direction of the test relative to the reference by saccading to one of the dots. Correct answers were rewarded with juice. Stimuli were at 100% coherence. Reference direction was fixed at 90°, and test directions ranged from -3° to $+3^\circ$ relative to the reference. Reference directions of 95° and 85° and coherence of 75%, 50%, 20% and 10% were used as controls (Methods). **(b)** Sample psychometric data shown for monkeys M and L. Probabilities of clockwise (CW) responses for various direction differences. The x-axis zero indicates the reference (upward, 90°) direction; positive values are clockwise deviations of test relative to reference, and negative values are counter-clockwise deviations. Error bars are s.e.m. in all figures. Gaussian distribution functions were fit to the data. Evaluated at the 80% level, psychometric thresholds are 1.7° and 2° (biases discounted).

discrimination performance of each neuron using an ideal observer analysis²⁵. Suppose a neuron's preferred direction were clockwise from the reference direction (Fig. 2a). Ideally, this neuron's firing rate for a clockwise test stimulus would be greater than its rate for the reference stimulus, which in turn would be greater than the rate for a counter-clockwise test stimulus. Therefore, an ideal observer monitoring the activity of this single neuron could predict that a clockwise test stimulus was presented in a given trial if the firing rate during the test were greater than the firing rate during the reference for that trial. The opposite rule would apply to a neuron tuned counter-clockwise from the reference. The probability of clockwise answers from the ideal observer can be calculated for each direction difference between -3° and $+3^\circ$ from the test and reference firing rate histograms for that difference (Fig. 2a; Methods). Note that for a direction difference of 3° —a difference reliably discriminated by the monkeys—the firing rate histograms for the test and reference stimuli considerably overlap, indicating poor neural discrimination performance. Fitting Gaussian distribution functions to these probabilities yielded neurometric functions (Fig. 2b), from which neural thresholds were estimated at the 80% level.

We computed the ratio of neurometric threshold to psychometric threshold for 240 neurons whose preferred directions ranged from 0° (right direction) to 180° (left direction) and included an upward component (Fig. 3a; Methods). A plot of the relative precision (that is, reciprocal of the threshold ratio) of these neurons as a function of their preferred direction relative to the reference direction (Fig. 3b)

showed a modest but reliable peak near 70° , as the precisions between 60° and 80° significantly differed from the rest (t -test, $P < 0.001$). The steepest part of the direction-tuning curve for the 240 neurons was located $67 \pm 1.4^\circ$ (mean \pm s.e.m.) away from the preferred direction. Consequently, the average neuron whose preferred direction was about 67° clockwise or counter-clockwise away from the stimulus direction had one of the steepest parts of its tuning curve near the stimulus direction (Fig. 3c and Supplementary Note 1 online). A sharp change in the tuning curve must result in a large difference between the test and reference responses and hence low discrimination thresholds. We tested this hypothesis by comparing the slope of the tuning curve near the stimuli directions with the discrimination threshold (Supplementary Fig. 1 online). Regression analysis showed that there was a robust and significant relationship between the two ($r = 0.46$, 99% confidence interval (CI) 0.40–0.51, $F = 241.8$, $P < 0.0001$). We also computed discrimina-

Figure 2 Neurometric functions. **(a)** Center, direction tuning curve of a neuron with a preferred direction of about 60° . Axes represent the firing rate of the neuron to stimuli moving in that direction (outermost circumference, 60 spikes/s). The left-pointing gray arrow indicates the reference direction. The right-pointing arrow indicates a direction clockwise from the reference. The firing-rate histograms for the reference and test intervals are black and gray, respectively. Left, trials in which the direction difference was 0° (test direction = reference direction); the black and gray histograms predominantly overlap. Right, direction difference of $+3^\circ$ (test direction = reference direction $- 3^\circ$). The degree of separation between the black and gray histograms gives a measure of the neurometric value for that direction difference (left, 0.5; right, 0.7; Methods). **(b)** Sample neurometric functions superimposed on the corresponding psychometric functions. Neurometric thresholds were estimated at the 80% level using bootstrap.

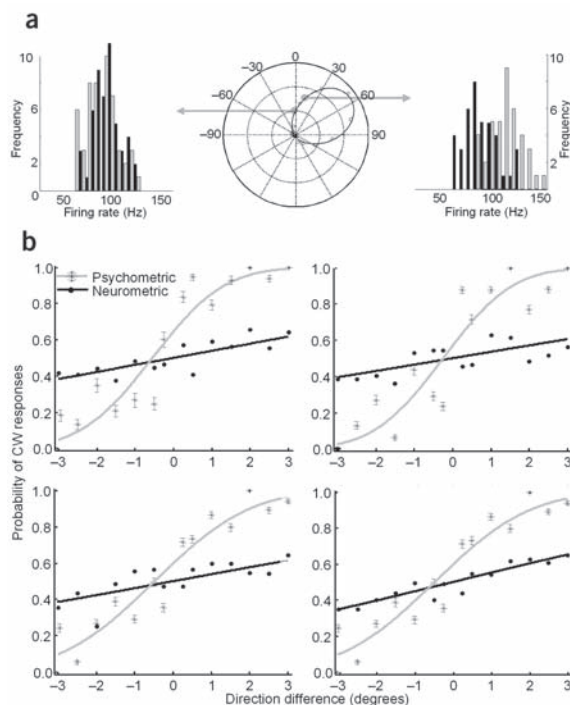


Figure 3 Relationship between neural precision and preferred direction.

(a) Neurometric-to-psychometric threshold ratio for 229 neurons for which a minimum of 15 trials were available at 12 or more direction differences. The average ratio is 26 ± 2.2 , and the minimum is about 2. (b) Relative precision (reciprocal of the threshold ratio) as a function of the neuron's preferred direction relative to the reference. (0° means neuron's preferred direction was in the reference direction, and 70° means neuron's preferred direction was 70° either clockwise or counter-clockwise from the reference direction.) Solid black line, moving average calculated every 4° within a 16° window. Dotted lines, s.e.m. Gray line, relative precision derived from the average direction-tuning curve of the 240 neurons (Methods). (c) Direction tuning curve of a neuron tuned 60° clockwise from the reference direction (black). Gray line, derivative of the tuning curve. One of the maxima of the slope occurs around the stimulus direction, indicating that this neuron has a low discrimination threshold.

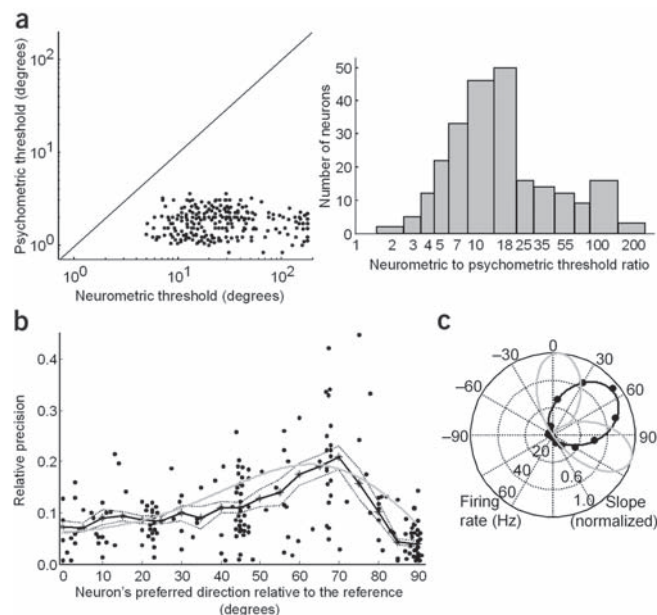
tion thresholds at different points on the average direction-tuning curve of the 240 neurons (Supplementary Note 1). We computed the relative precision using the average psychophysical threshold of 1.7° (Fig. 3b). The two estimates of precision predominantly overlapped ($r^2 < 0.1$), indicating that discrimination thresholds are lowest for neurons whose preferred directions flank the stimuli to be discriminated, in agreement with previous studies of fine discrimination^{8,16,26–30}.

Covariation of neural response and monkeys' choices

To determine which parts of the neural population response are significantly correlated with the decisions, we assessed the degree of covariation between the neural response and the monkey's choices in the trials in which the direction differences were small (-0.5° to 0.5°). If all neurons in a population contribute equally to the decisions, then the monkey's decisions must covary with the activity of each neuron in this population to the same degree. If instead the lower envelope principle were correct^{1,6}, then the responses of a small group of neurons in the population must exhibit a larger degree of covariation with the monkey's choices compared to the rest of the neurons (see Methods for the effect of interneuronal correlations on these tests).

We first used 'choice probability' as the measure of covariation. The choice probability of a neuron is the average accuracy with which an ideal observer can predict the monkey's choice in a trial using the neuron's response¹⁹. A choice probability of 0.5 indicates that the neuron's responses carry no predictive power for the monkey's choices and that the neuron may not be involved in computing decisions. A choice probability of 1.0 indicates that the neuron accurately predicts the monkey's choices. Consider only those trials in which direction differences were very small (Methods). Suppose a neuron's preferred direction were clockwise from the reference direction. Because the direction differences are small, the reference and test responses of this neuron must ideally be about the same. However, these responses fluctuate randomly from trial to trial. If this neuron were associated with the monkey's decisions, then the monkey would probably choose a 'clockwise answer' when there is either a random increase in the test firing rate or a random decrease in the reference rate or both. Similarly, the monkey might choose a 'counter-clockwise answer' when there was either a random decrease in the test firing rate or a random increase in the reference rate or both.

We computed choice probabilities in three ways. First, we ignored fluctuations in the reference firing rates and considered only fluctuations in the test firing rates. For each neuron, we grouped the test rates into one histogram for clockwise choices and another for counter-clockwise choices. Given a sample test firing rate from each of the two histograms, an ideal observer could predict the monkey's choices as follows. If the neuron's preferred direction were clockwise from the reference, then the greater of the two firing rates must come from the trial in which the



monkey chose a clockwise answer. The probability of correct answers for this ideal observer, which is the choice probability, was calculated using this rule (Methods). The average choice probability was 0.55 (Fig. 4a), significantly greater than chance (t -test, $P < 0.0001$, 99% CI 0.53–0.56), implying that these neurons were associated with the monkeys' discrimination decisions¹⁹. Second, we ignored fluctuations in the test firing rates and considered only the fluctuations in the reference rates. Following the same procedure as above, but appropriately modifying the decision rule (Methods), we estimated that these choice probabilities had an average of 0.52 (Fig. 4b), significantly greater than chance (t -test, $P < 0.002$, 99% CI 0.51–0.53). Finally, we computed choice probabilities by taking into account both reference and test firing rates together. The average value was 0.52 (Fig. 4c), significantly greater than chance (t -test, $P < 0.0001$, 99% CI 0.51–0.53). Regression analysis (Fig. 4d) showed a subtle but significant positive correlation ($r = 0.042$, 99% CI 0.030–0.054, $F = 50$, $P < 0.00001$) between the test-only choice probability values (Fig. 4a) and neural precision, indicating that neurons with higher precision had a greater predictive power for the monkey's choices. Similar results were obtained for the reference-only choice probabilities ($r = 0.01$, 99% CI 0.008–0.02, $F = 8$, $P < 0.02$) and the test-and-reference combined choice probabilities ($r = 0.02$, 99% CI 0.011–0.032, $F = 15.4$, $P < 0.0001$).

The test-only choice probabilities (Fig. 4a) for neurons tuned within 30° of the reference direction was 0.51 (first bin in Fig. 4e), not significantly different from chance (t -test, $P > 0.2$). The average choice probability for neurons tuned around 67° (peak in Fig. 3b) was the highest, at 0.57 and significantly above chance (t -test, $P < 0.0001$). For choice probabilities in Fig. 4b and c, the same pattern of results was obtained. The average choice probability in the first bin was not significantly different from chance (0.5; $P > 0.8$ and 0.5; $P > 0.3$, respectively) and the average choice probability in the fifth bin was the highest among all bins, and significantly different from chance (0.53; $P < 0.01$ and 0.54; $P < 0.0001$, respectively).

We used mutual information^{31,32} as a second measure of the covariation between neural activities and decisions. Consider the ideal example of a neuron whose firing rates accurately predict the monkey's choices. An observer informed only of this neuron's firing rate in a trial gains $\log_2(2) = 1$ bit of information about which of the two choices the monkey would make. In this sense, a neuron with mutual information of 0 bits conveys no information (to the ideal observer or another

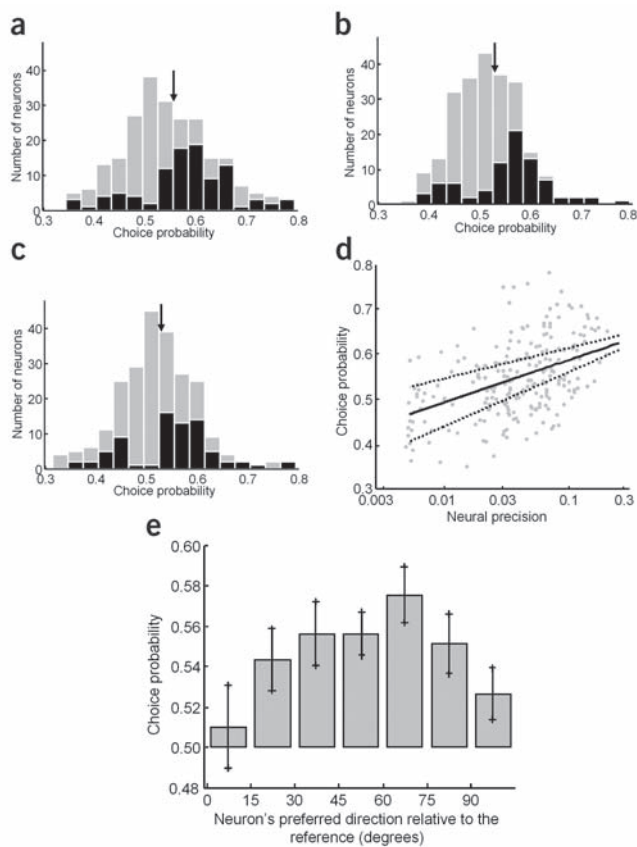


Figure 4 Covariation between neural responses and the monkeys' choices. **(a)** Histogram of choice probabilities calculated by pooling test firing rates from trials in which the direction deviations ranged from -0.5° to $+0.5^\circ$. Black arrow, average, 0.55. Shaded parts of the bars, neurons with individually significant choice probability in a permutation test¹⁹. **(b)** Histogram of choice probabilities calculated from the reference firing rates alone. **(c)** Histogram of choice probabilities calculated from both the reference and test firing rates. **(d)** Choice probabilities in **a** plotted against neural precision. Black line, regression; dotted lines, 99% confidence interval for the estimate of the slope. **(e)** Choice probabilities in **a** as a function of the preferred direction of the neuron relative to the reference.

neuron that reads out its responses), whereas a neuron with mutual information of 1 bit conveys all the information about the decision. We computed the mutual information between each neuron's firing rates and the monkey's choices (Methods). The population-average mutual information (**Fig. 5a**) was $0.34 \text{ bits} \pm 0.01$, significantly greater than 0 ($P < 0.0001$). A plot of this mutual information as a function of the neuron's preferred direction relative to the vertical (**Fig. 5b**) showed that the mutual information peaked for neurons whose preferred directions were about 60° away from the reference direction. The mutual information values within a 30° bandwidth around the 60° peak were significantly different from the rest of the mutual information values (t -test, $P < 0.0001$). This mutual information was calculated only from the trials in which the direction differences were zero. For the smallest direction difference of 0.125° (**Fig. 5b**, bottom), the information conveyed by the stimuli about the decision was significantly lower than that conveyed by the neurons about the decision (t -test, $P < 0.0001$). This test rigorously showed that the correlation between the neuron's activity and decisions did not result spuriously from a correlation between

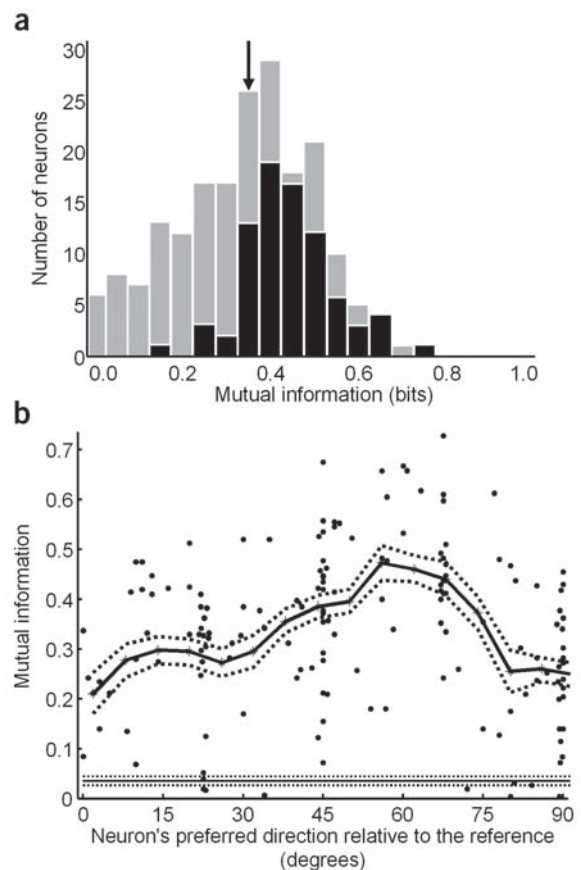


Figure 5 Mutual information between neuron's firing rates and the monkeys' decisions. **(a)** Histogram of mutual information calculated from the reference and test firing rates from the ambiguous trials only (direction difference = 0°), for 211 neurons for which both conditional probability density functions could be estimated (Methods). Shaded parts of the bars, neurons with individually significant mutual information in a permutation test. **(b)** Black dots show the mutual information between neuron's response and monkey's decision as a function of the neuron's preferred direction relative to the reference. Black line, moving average calculated every 4° within a 16° window. Dotted lines, s.e.m. Black horizontal line (bottom), mutual information between the stimuli and decisions for the smallest stimulus cue of 0.125° . Dotted lines, s.e.m.

the stimuli and decisions. Hence the peak in the mutual information reflected a genuine difference in the amount of information conveyed by different MT neurons in the population.

Comparison of neural and psychophysical performance

The relative contribution of each active neuron to the decision was alternatively assessed by an independent modeling exercise using neural responses and interneuronal correlations estimated from the data. We evaluated various neural coding schemes ranging from single-neuron, labeled-line models to coarse population codes for their ability to reliably produce the observed psychophysical performance. A generic discrimination model in which the neurons were split into clockwise and counter-clockwise pools was used (**Fig. 6a**). Within each pool, activities of the neurons were combined through Quick³³ pooling: the i th neuron's activity was scaled by a factor of v_i and non-linearly transformed by an exponent α (Methods). The transformed activities were summed and non-linearly compressed with an exponent of $1/\alpha$. The pooled clockwise and counter-clockwise activities were then compared

to make a decision in favor of the pool with the greater pooled activity. Each neural response was obtained by sampling our neural database with replacement (Methods). Every pair of neural responses was sampled with an average correlation of 0.12 (estimated from our multi-electrode data). Fifteen trials were simulated for each direction difference (from -3° to $+3^\circ$). A neurometric function was fit. The threshold and the residual (sum squared) error of fit were both estimated. This simulation was repeated 100 times, and the average threshold and residual error were computed for each neural code.

Different neural codes were simulated by varying the pool size N , the pool constitution as determined by the weighting factors v_i and the pooling non-linearity α . For example, setting $v_i = 1$ for all i , and $\alpha = 1$, yielded a broad, non-selective, linear decision pool²⁰. Setting $v_i = 1$ for the most precise neuron in the pool and $v_j = 0$ for the rest of the neurons, simulated the lower envelope principle^{1,6}. In between these two extremes, different population codes were simulated with different choices for v_i . In each case, increasing values of α yielded progressively greater non-linear pooling, with large values of α resulting in a winner-take-all selection of only the neuron with the highest activity in the pool³³. The performance of a broad equal-weight neural-pool (Fig. 6b), at low degrees of non-linearity ($\alpha = 1$ and 2, linear and quadratic cases), was 3 times less precise than the psychophysical performance even for very large pool sizes ($N > 2000$). At higher degrees of non-linearity, the neural performance asymptotically ($N > 150$) approached the psychophysical performance. However, the corresponding residual error also increased (Fig. 6c), resulting in a decrease in the reliability of the decisions due to the winner-take-all amplification of noise³³. Next, we used three different weight-

ing schemes (exponential, Cauchy and Gaussian) to assign higher weights to the activities of neurons at the peak (70°) and progressively lower weights for neurons tuned away from the peak (Methods). For all 3 weighting schemes, the neural performance asymptotically ($N > 200$) approached the psychophysical performance while the residual error remained bounded with increasing pool size (Fig. 6d,e). These results were obtained for a wide range of values of α . We repeated the simulations by keeping the multiplicative weights same for all neurons, de-emphasizing the activities of neurons tuned around the reference through compressive non-linearities ($\alpha < 1$) and preserving the activities ($\alpha = 1$) of those tuned 60° away. We obtained the same pattern of results for this method. Finally, we used probability summation instead of additive pooling to combine the activities. In this case, performance was uniformly poor for all neural codes, in agreement with a previous study²⁰.

The lowest neuron-to-behavior threshold ratio in our sample was about two. Because we uniformly sampled neurons tuned to all directions, the sample size for any given direction was limited. Hence we cannot rule out the presence of neurons of even greater precision. It is possible that the inclusion of neurons with greater precisions than found in our sample may yield a broader non-selective decision pool whose performance matches the psychophysical performance. However, our sample was large enough to provide an accurate estimate of the true average precision of neurons tuned upward over 180° . This average precision was 26 ± 2.2 times lower than that of the monkeys'. Hence broad non-selective pooling of our sample of neurons was inadequate to explain the psychophysical performance.

DISCUSSION

Single neuron precision for fine discrimination

Our sampled neurons have poor ideal-observer performance for fine discrimination when compared to the exquisite performance reported for a coarse discrimination task in which monkeys identified two opposite directions of motion^{17,18}. Does this reflect a difference in the inherent capacity of MT neurons for fine and coarse discrimination? A major part of this difference is due to the sampling procedure. Because our aim was to compute the perceptual contribution made by each neuron in the distributed population, we did not limit our sampling

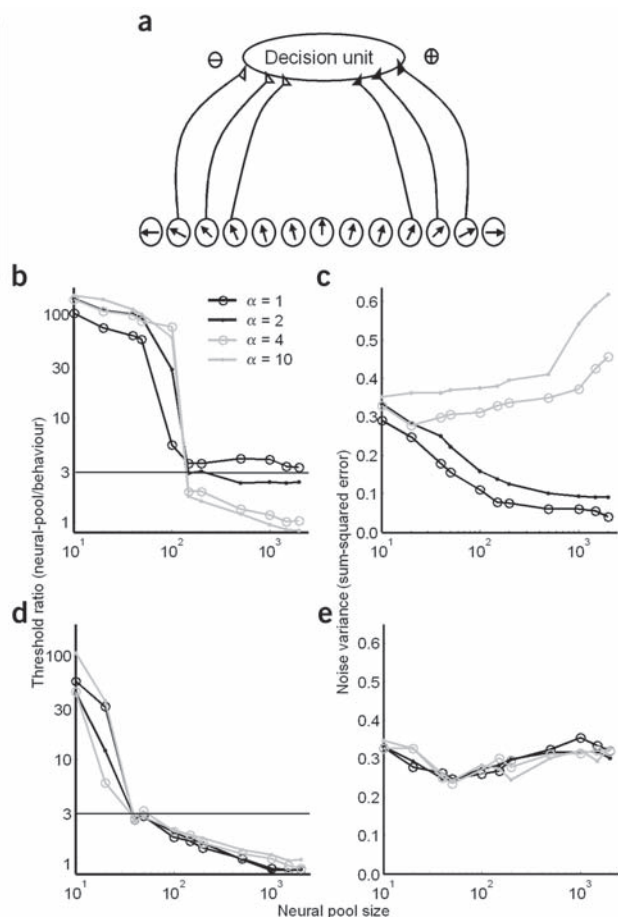


Figure 6 Fine discrimination performance of various neural coding schemes analyzed using a discrimination model. **(a)** Network for computing discrimination decisions. Bottom row shows MT neurons; arrows indicate preferred direction of motion. Filled synapses are excitatory, and open synapses inhibitory. The most precise neurons are tuned around 66° away from the reference (upward) direction. Activities are pooled within each group using Quick pooling, and the difference between the two group activities determines the decisions. Positive differences generate clockwise decisions, and negative differences generate counter-clockwise decisions. **(b)** Neural-pool to behavior threshold ratio is shown for uniform, non-selective pooling of the activities of all the neurons tuned in all 90° on either side of the reference direction. Linear and quadratic pooling yield a performance that is about three times less than the psychophysical performance, even for pools with 2000 or more neurons. Higher degrees of non-linearity yield performance that matches the psychophysical performance. **(c)** Noise variance of the same pooling schemes. The noise variance decreases with increasing pool size only for the linear and quadratic cases. For higher degrees of non-linearity, the noise variance increases with increasing pool size. **(d)** Neural pool to behavior threshold ratio for the pooling scheme that selectively emphasizes the activities of neurons tuned 70° away from the reference. Neural pool's performance matches the psychophysical performance for pools of about 250 neurons or more, for a wide range of non-linearities. **(e)** In this case, the noise variance remains bounded with increasing pool size.

to the most precise neurons, as did the previous studies^{17,18}. Therefore, the average threshold ratio obtained in our study was 26, whereas the average ratio obtained in the coarse discrimination studies was close to 1.0. However, the most sensitive neurons in the coarse discrimination study were at least 10 times more sensitive than the monkeys, whereas the most precise neurons in our study were 2–3 times less precise than the monkeys. Such a large difference is unlikely to be due to the difference in sampling procedure alone. Therefore, in **Supplementary Note 2** and **Supplementary Figs. 2–7** online, we consider several other factors, such as the use of a two-interval task, the use of a small range of direction differences, which necessitated an extrapolation of the neurometric functions to estimate thresholds, and the use of a stimulus duration of 1 s instead of 2 s (refs. 17, 18). This comparison indicates that these factors might account for a small part of the difference in the results, but not all of it. Hence it seems likely that MT neurons have an inherently poor capacity for fine discrimination. One reason for this poor fine-discrimination ability could be the broad width of MT direction-tuning curves. According to estimation theory, tuning width and the background activity level are the primary factors that influence discrimination thresholds in a wide range of models³⁴.

Two independent observations validate our threshold measurements. First, the best psychophysical orientation discrimination thresholds are about 1–2°, and the average orientation-tuning width of monkey V1 neurons²⁸ is about 40°. In contrast, the best psychophysical direction discrimination thresholds are about 1–2°, whereas the average direction-tuning width of MT neurons¹⁶ is about 100°. Because the most precise V1 neurons (2/50) have a threshold ratio²⁸ slightly greater than 1.0, we can expect MT neurons also to have a threshold ratio greater than 1. Second, direction-discrimination thresholds computed from MT direction-tuning data in anesthetized monkeys³⁵ were 7.5° in very few neurons, with a mean ($n = 36$) threshold of 35°. The lowest neural threshold in our data was 5°, and roughly 10% of our neurons had a threshold of 7.5° or lower. Our mean ($n = 229$) threshold was 37°. Therefore these two studies are mostly in agreement (though we estimated thresholds at 80% correct, whereas the other study used 69%).

Covariation of neural response and choice

Both test and reference responses, independently and together, showed significant covariation with the monkeys' choices. The average choice probability for test responses was 0.55, the same value obtained in the coarse discrimination study¹⁹. The average choice probability for reference rates alone and for test and reference rates together was 0.52. Unlike test responses, reference responses must be stored and retrieved before they are used to compute decisions. Therefore, additional noise may corrupt the reference firing rates. The lower values of the two choice probabilities calculated using the reference firing rates could be due to this noise. A choice probability value of 0.52 has been reported for MT neurons in a speed discrimination task (J. Liu & W.T. Newsome, *Soc. Neurosci. Abstr.* 438.4, 2003).

Pooling efficiency of the decision network

Most MT neurons are at least as sensitive as the monkeys in a coarse discrimination task in which monkeys discriminate between two opposite directions of motion. Modeling shows that four to eight neurons suffice to account for the monkey's performance¹⁸. However, a low choice probability value of 0.55 for this task indicates that a pool of about 70–100 neurons is involved in computing the decisions^{19,20}. Several explanations for this discrepancy have been proposed: that decision networks may inevitably form broad non-selective pools that include low-sensitivity neurons due to anatomical limitations²⁰, that

additional pooling noise postsynaptic to MT neurons may reduce the choice probability²⁰, or that the integration period used for neural responses may have been longer than the time it took the monkeys to make decisions³⁶. In a reaction-time motion detection task, single MT neurons have lower precision than the monkey³⁷, indicating that pooling is necessary. Our results show that in the fine discrimination task, selective pooling is necessary and that the decisions are associated with the activities of high-precision MT neurons to a greater extent than with those of the low-precision neurons. Several neural mechanisms implicated in perceptual learning can mechanistically modify an initially inefficient decision network to focus on the activities of task-relevant neurons^{38–41}. Further modeling studies will show whether or not the precision, choice probability, mutual information and correlation values for the fine discrimination task are consistent with each other.

METHODS

Behavioral methods. Monkeys fixated on a central dot while the stimuli (random dot kinematograms, 3 dots/deg², 0.1° diameter dots, 42 cd/m² luminance, background 2 cd/m², average dot lifetime 0.260 s) were presented within the receptive fields of MT neurons. For the data reported here, the random dot kinematograms were at 100% coherence, but lower coherence values appeared intermixed with these trials (unpublished data). **Supplementary Note 2** describes controls in which the reference direction was jittered. Eye movements were monitored through scleral search coils⁴². The trial was aborted if the eyes moved outside a 0.5° square. Direction differences of ±3°, ±2.5°, ±2°, ±1.5°, ±1°, ±0.5°, ±0.25°, ±0.125° and 0° were used. (Negative differences refer to counter-clockwise tests.) Each direction difference was presented 20 times, randomly intermixed with all others. Direction tuning of each neuron was estimated by roughly determining its preferred direction, followed by taking 8–10 samples at each of 8 equally spaced directions on either side of this rough estimate of the preferred direction. For the first 28 of the 240 neurons, we took only three to four samples at each of four equally spaced directions on each side. (One of these is shown in **Fig. 3c**.)

Physiological methods. Animal procedures were approved by the University of Chicago's Institutional Animal Care and Use Committee and were in compliance with NIH guidelines. We used 3–12 polyimide-sheathed electrodes (125 μm diameter; FHC, ME) to record from several MT neurons simultaneously. Neural signals were recorded using a 92-channel system (Multichannel Acquisition Processor, Plexon, TX; **Supplementary Note 3**). The Horsely-Clark coordinates of the recorded locations ranged from 4–5 mm posterior and 15–16 mm lateral. We ascertained the recording locus to be MT from the physiological properties of the neurons^{14,15}. The preferred location, size and speed (to within two octaves⁴³) of the stimuli were matched to those of the neurons on all the electrodes. If the receptive fields of the neurons had very dissimilar spatial and speed preferences, we recorded only from one of the neurons. This filtering process ensured that all simultaneously recorded neurons had the same preference for location, size and speed, but not necessarily for direction. The maximum number of simultaneously recorded neurons was 13, the minimum was 1, and the average was 2.25. The results presented here are for 240 neurons whose preferred directions ranged from 0° (right direction) to 180° (left direction), and included an upward component (but see 'Choice probabilities' below).

Neurometric analysis. Suppose a neuron's preferred direction is clockwise from the reference direction. An ideal observer could consistently predict a clockwise test (counter-clockwise test) for all trials in which the firing rate for the test interval is greater (lower) than that for the reference interval. The average performance of this ideal observer for each direction difference can be evaluated (**Fig. 2a**). The firing rates from the reference interval are grouped together into a histogram that provides (when normalized) an estimate of the conditional probability density of the firing rate given that the stimulus direction is equal to the reference direction, $p(r/REF)$. Similarly, the firing rates from the test interval (test direction is 3° clockwise from reference direction for the example shown) are grouped into another histogram, whose normalized value provides an estimate of the conditional probability density for the firing rates given the 3°

clockwise-deviated test, $p(r/CW)$. The probability of clockwise answers for the ideal observer equals the probability of the firing rate from the test interval being greater than the firing rate from the reference interval, which is given by

$$\int_0^{\infty} \int_0^{\infty} p(s/CW) ds \int_0^{\infty} p(r/REF) dr$$

As the test direction becomes closer to the reference direction, the two histograms predominantly overlap. Hence the probability of 'clockwise answers' from the ideal observer approaches chance. If the test direction is counter-clockwise to the reference, then the test histogram will lie to the left of the reference histogram. Therefore the probability of 'counter-clockwise answers' ($1 - \text{probability of clockwise answers}$) will increase above 0.5. Repeating this calculation for all direction differences yielded neurometric values to which a Gaussian distribution function was fit.

Choice probabilities. Test firing rates were grouped into one histogram for clockwise decisions and one for counter-clockwise decisions from trials in which the test direction was the same as the reference direction. Hits and false alarms were decided from the neuron's direction preference, as explained in the text. The area under the receiver-operator characteristic (ROC) curve for this histogram pair gave the choice probability. The mean choice probability for all the 240 neurons was 0.55, significantly greater than chance (t -test, $P < 0.0001$, 99%CI 0.52–0.58). This calculation was repeated for each non-zero direction difference in the range -0.5° to 0.5° . A two-way ANOVA showed that neither the magnitude of direction difference ($F_2 = 1.14$, $P = 0.29$) nor the direction of the test relative to the reference (clockwise or counter-clockwise; $F_2 = 1.48$, $P = 0.22$) had a statistically significant effect on the choice probabilities. The pooled choice probabilities for non-zero direction differences did not differ significantly from the choice probabilities for the ambiguous stimulus (t -test, $P > 0.87$). Therefore, more reliable estimates for choice probabilities were obtained by pooling the firing rates for direction differences in the range -0.5° to $+0.5^\circ$, inclusive of 0° . This pooling gave 150–200 trials per neuron, more than the minimum required¹⁹. These 'grand estimates' of choice probabilities are shown in Fig. 4a. Their average was 0.55, significantly greater than chance, and had tighter confidence intervals compared to the average choice probability for the ambiguous stimuli alone (0.53–0.56). Choice probabilities for the reference firing rates were calculated in a similar manner, with the complementary decision rules.

Choice probabilities in Fig. 4c were calculated by providing the ideal observer with the difference between the test and reference firing rates (test rate – reference rate) for two trials, one in which the monkey made a clockwise choice and another in which it made a counter-clockwise choice. If the neuron was tuned clockwise from the reference, then the greater of the two differences must come from the trial in which a clockwise answer was chosen. (The complementary rule was applied to neurons tuned counter-clockwise.) One caveat of using covariation measures to identify the decision pool is that interneuronal correlations may diminish the power of these tests. Suppose a neuron is not used in the decision-making process, but its response is correlated with that of another neuron that is used in computing the decisions. Then the responses of the neuron not used in decision-making may still exhibit a significant covariation with the monkey's choices. Interneuronal correlations were estimated from the data in order to evaluate their effect on the estimates of covariations (see below).

In addition to the 240 neurons reported, we obtained 42 neurons whose preferred directions included a downward component (ranged between 180° and 360°). The average choice probability of these 42 neurons was 0.51, not significantly different from chance (t -test, $P > 0.38$). This is why we have postulated a simplified discrimination model consisting only of neurons whose preferred directions included an upward component.

Mutual information. Suppose the monkey makes clockwise and counter-clockwise choices with equal probabilities. The *a priori* uncertainty about the monkey's choice in any given trial, $H(C)$, is 1 bit. Increasingly large positive differences between the test and the reference firing rates for a 'decision' neuron tuned clockwise of the reference direction predict a clockwise decision from the monkey with increasing certainty. No uncertainty would remain about the decision made in a trial once it became known that the difference, test rate – reference rate, was a large positive value in that trial, that is, $H(C/FR) \approx 0$. Therefore,

for a clockwise-tuned 'decision' neuron, a full 1 bit of information is gained about the monkey's decision by knowing that the firing-rate difference was a large positive value. Small differences in the firing rate convey little information about the decision made (probability of clockwise answers ≈ 0.5). Mutual information is the average information gained about a monkey's choice in a given trial from knowledge of the firing rates. However, some clockwise-tuned neurons may exhibit the opposite behavior: test firing rates may be consistently lower than reference firing rates in the trials in which the monkey chose clockwise answers. In the choice-probability analysis, we found that neurons with statistically significant negative correlations between firing rates and choices were a small minority, about 6% of all our neurons. Therefore, we first calculated mutual information as described below for all neurons. We found that eliminating the neurons with significant negative correlations did not change the results shown in Fig. 5. (The peak was still significant and located at 65° .)

The probability distribution of the choices and the conditional distributions of the decisions given the firing rates were estimated from the ambiguous trials. Mutual information was calculated as $I(FR, C) = H(C) - H(C/FR)$, where $H(C)$ is the entropy of the choices and $H(C/FR)$ is the conditional entropy of the choices given the firing rates^{31,32}. Next, we calculated $I(C, FR) = H(FR) - H(FR/C)$, where $H(FR)$ is the entropy of the firing rates and $H(FR/C)$ is the conditional entropy of the firing rates given the choice. Note that $I(C, FR) = I(FR, C)$. The two estimates did not differ significantly ($P > 0.7$). Fig. 5 shows the average of the two estimates.

Computational analysis. Consider a generic discrimination model (Fig. 6a). Let CW_i be the activity of the i th clockwise neuron and CCW_i be the activity of the i th counter-clockwise neuron. The combined activity of the neural decision pool can be represented by the general discriminant function³³

$$D = \left[\sum_{i=1}^{N/2} (v_i CW_i)^\alpha \right]^{1/\alpha} - \left[\sum_{i=1}^{N/2} (v_i CCW_i)^\alpha \right]^{1/\alpha}$$

where the clockwise and counter-clockwise pools each have $N/2$ neurons (the total pool size is N), v_i is a weighting factor for the i th neuron and α is a measure of the pooling non-linearity. Let $d(i) = |\text{preferred direction of the } i\text{th neuron} - \text{reference direction}|$. We used exponential ($v_i = \exp[-|d(i)-70|/\sigma]$), Cauchy-like ($v_i = 1/[1+|d(i)-70|^2]$), and Gaussian-like ($v_i = \exp[-(|d(i)-70|/\sigma)^2]$) weighting schemes to assign higher weights to the activities of neurons tuned about 70° away from the reference direction and lower weights for the other neurons. The discriminant D was computed by sampling neural responses with an average correlation of 0.12 (estimated from the data; see next section) from our neural database with replacement. If $D > \gamma$, then a clockwise test was predicted; if $D < -\gamma$, then a counter-clockwise test was predicted; if $-\gamma < D < \gamma$, then a random prediction was made with equal probability for clockwise and counter-clockwise tests. γ is an uncertainty factor⁴⁴. We computed network performances for direction differences from -3° to $+3^\circ$. A neurometric function was fit to the results. The neural threshold and the residual error of fit (the sum squared error) were estimated.

Interneuronal correlations. For each direction difference, correlation between the z -scores was calculated for 420 neuronal pairs⁴⁵. A two-way ANOVA showed that neither the magnitude nor the sign of direction difference had a statistically significant effect on the correlations. Therefore, we pooled data across all direction differences and obtained a 'grand' average correlation of 0.12 ± 0.01 , significantly different from 0.0 (t -test, $P < 0.0001$). This value was used in the simulations. In simulations, the effect of removing the correlation on the covariation measures was that the high-precision neurons showed slightly higher covariations and the low-precision neurons showed significantly lower covariations. (Mutual information for neurons tuned around the reference dropped to 0.0.)

Note: Supplementary information is available on the Nature Neuroscience website.

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The authors declare that they have no competing financial interests.

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