

Dynamics of neuronal responses in macaque MT and VIP during motion detection

Erik P. Cook and John H. R. Maunsell

Howard Hughes Medical Institute and Division of Neuroscience, Baylor College of Medicine, Houston, Texas 77030, USA

Correspondence should be addressed to E.P.C. (erik@cns.neusc.bcm.tmc.edu)

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We examined how the relationship between neuronal activity and behavior evolved over time during a motion-detection task. Recording from two regions of visual cortex that process motion, the middle temporal (MT) and ventral intraparietal (VIP) areas, we used the time it took subjects to detect a motion stimulus to evaluate the dynamics of the underlying neuronal signals. Single-neuron activity was correlated with stimulus detection and reaction time (RT) in both areas. The rising edge of the population response from both areas was highly predictive of RT using a simple threshold-detection model. The time course of the population responses, however, differed between MT and VIP. For MT, the onset of the neuronal response was relatively constant, whereas for VIP the onset of the neuronal responses increased with RT. In contrast to previous studies, we found that single neurons were not reliable detectors of the motion signal when constrained by realistic detection times.

How does the relationship between activity in visual cortex and the perception of visual stimuli evolve over time? We addressed this question by measuring the activity of individual neurons while subjects performed a motion-detection task. The goal was to determine the time course and characteristics of the neuronal response that supported behavioral performance.

Understanding which portion of the neuronal response underlies behavior is important for quantitatively linking neuronal activity to perception. Many studies have examined the relationship between the activity of neurons in visual cortex and perceptual capabilities (for example, refs. 1–3); some have measured neuronal activity and behavioral performance simultaneously (for example, refs. 4–6). The conclusion from many of these studies, and those from other sensory modalities (for example, ref. 7), is that the activity of single neurons can account for, or approximate, the perceptual abilities of the subjects⁸. In many of these studies, the behavioral report was separated in time from the stimulus presentation, and neuronal responses were usually characterized using spike counts occurring in a fixed time window. Thus, it is difficult to deduce from these studies which portion of the neuronal response was most closely linked to the behavior.

Psychologists have long used reaction time (RT) as a tool for understanding the stages of mental computation that support a given perceptual task^{9,10}. Recordings from the frontal eye fields (FEF) have suggested that RT variability in a sensorimotor task is due primarily to the variability in the response preparation stage rather than to perceptual processing in visual cortex¹¹. If this is true, neuronal activity in visual cortex should have little or no relationship to RT.

Here we investigated how neuronal activity develops over time during the detection of motion. Recording from MT and VIP in

two monkeys, we found that neuronal responses in both areas were correlated with detection and RT on a trial-by-trial basis. When neuronal responses from many cells were grouped by RT, a simple threshold model accounted for behavioral performance and provided an estimate of the temporal window used to detect the motion. Using this temporal window, we found that single neurons were not reliable motion detectors. On average, the performance of individual neurons in both areas was far poorer than the detection capabilities of the subjects.

RESULTS

Two monkeys performed the motion detection task illustrated in Fig. 1. While the animal pressed a lever and fixated on a central point, two patches of dynamic random dots were presented on opposite sides of the fixation point. Both patches started with no net motion (0% coherent), and the animal's task was to release the lever within 750 ms after either patch began moving in a coherent fashion. Coherent motion started at a random time, and the animal was cued at the beginning of every trial as to which patch would contain the coherent motion. One patch of dots filled the receptive field (RF) of the neuron under study, and the coherent motion was set to match the neuron's preferred direction and speed. Three levels of coherent motion were randomly interleaved.

The reason we used two patches of random dots was to also study the effects of attention on the responses of MT and VIP neurons. Those results are reported elsewhere¹². In the current study, we used only trials in which the animal's attention was directed to the patch of random dots located in the RF.

We recorded from neurons in MT and VIP, two regions of the visual cortex involved in motion processing. Data from a representative MT neuron are shown in Fig. 2. As the coherent motion strength increased, neuronal responses increased and detection



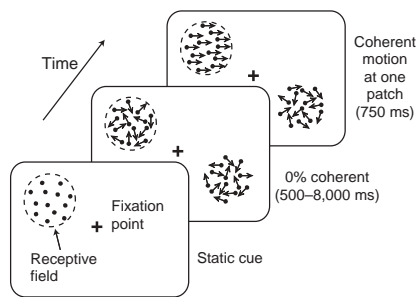


Fig. 1. Motion detection task. A trial began with the presentation of the fixation point and cue of stationary dots indicating which patch would most likely contain the coherent motion. Once the animal fixated and pressed a lever, dots in both patches began moving with 0% coherent motion. At a random time (between 500 and 8,000 ms), one patch began moving coherently and the animal had a RT-window of 200 to 750 ms to release the lever to obtain a reward. Motion times were exponentially distributed with a mean of 1,300 ms (except for 21 MT cells that had a uniform distribution). The strength of the coherent motion was varied randomly from trial to trial among three preset levels to produce a range of behavioral performances. Only trials in which the cue and the coherent motion appeared in the RF of the neuron (as illustrated here) were used for this study.

performance improved (Fig. 2a). At the low motion coherence (12.5%), the monkey correctly detected the motion signal on 60% of trials (below horizontal line). For stronger motion coherences of 17.5 and 25%, the monkey's behavioral performance was 95 and 100% correct, respectively. Across all experiments, the average behavioral performance was 50, 92 and 99% correct for low, medium and high coherence trials, respectively.

Covariation of neuronal response and RT

For each level of coherent motion, the monkey's RT varied. We examined whether the neuron's response was correlated with the time it took the monkey to respond to the coherent motion. Neuronal responses were first smoothed by convolving each raster with a low pass exponential filter ($e^{-t/\tau}$) with $\tau = 100$ ms. This filter was chosen to mimic the way neuronal signals may have been integrated by the monkey to detect the coherent motion. Our results, however, were not sensitive to the shape or time constant of our filter. The Pearson's correlation coefficient (ρ) between RT and the smoothed neuronal response was calculated as a function of time using the correct trials (Fig. 2a, below each raster). Although ρ is noisy, there is a suggestion that this cell has a weak but consistent negative correlation with RT after the coherent motion starts. That is, RTs tended to be shorter when the neuronal response to motion was stronger.

To see if a negative correlation existed across our sample of MT and VIP neurons, we computed the average correlation coefficient between neuronal response and RT for each level of motion coherence (Fig. 3). During 0% coherent motion, there was no systematic relationship between neuronal responses and RT. After the coherent motion began at time zero, there was a consistent negative correlation between neuronal activity and RT that peaked around 200–300 ms. This suggests that the relationship between neuronal activity and RT is strongest soon after the coherent motion begins, but then weakens before the lever is released. Thus, the early portion of the coherent motion may be the most important in determining the monkey's response. Notably, the correlations for VIP are larger and peak later than those for MT.

Covariation of neuronal responses and detection

Did the neuronal responses predict whether the stimulus would be detected? On average, both MT and VIP responses were weaker on trials where the animals failed to respond to the coherent motion. Choice probability is a statistical measure that has been

Fig. 2. Example MT neuron. (a) Spike rasters and RT correlation. Each raster plot corresponds to a different coherent motion strength. Each raster row is a single trial aligned at the onset of the coherent motion, which is marked by the vertical line at time zero. Each tick mark represents the occurrence of one action potential. To the left of the vertical line is the response to the 0% motion and to the right is the response to the coherent motion. Trials in which the monkey released the lever within the RT window (correct trials) are shown below the horizontal line in each raster plot, while trials in which the monkey failed to release the lever in response to the coherent motion (missed trials) are shown above. Correct trials are sorted by RT, with the time of lever release indicated by the heavy mark at the end of each trial. No trials were missed for the high-coherence condition. RT correlation (ρ) for each motion coherence is shown below each raster and is the correlation coefficient between the time of lever release and the smoothed neuronal responses (using an exponential filter with $\tau = 100$ ms). A negative ρ indicates that shorter RTs were associated with increased neuronal response. (b) Time course of detect probability for the low coherent motion only. Detect probability was computed at 5 ms intervals using the smoothed responses from the low coherent raster as described for choice probability¹⁴. A detect probability of 0.5 indicates chance ability to predict behavioral outcome from the neuronal response; a detect probability of 1.0 indicates the distributions are completely separate and behavioral outcome is perfectly predicted from the neuronal responses. All plots extend to the median RT for each condition.

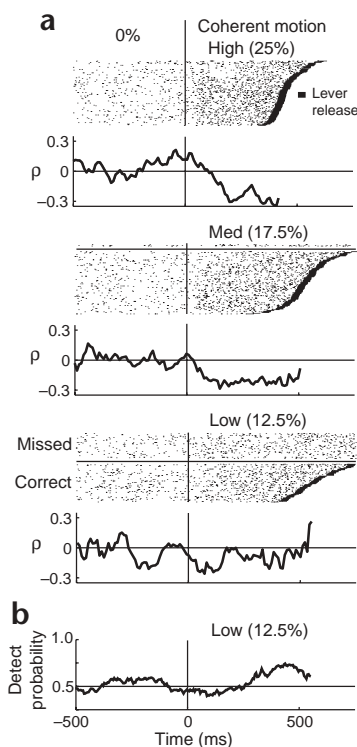
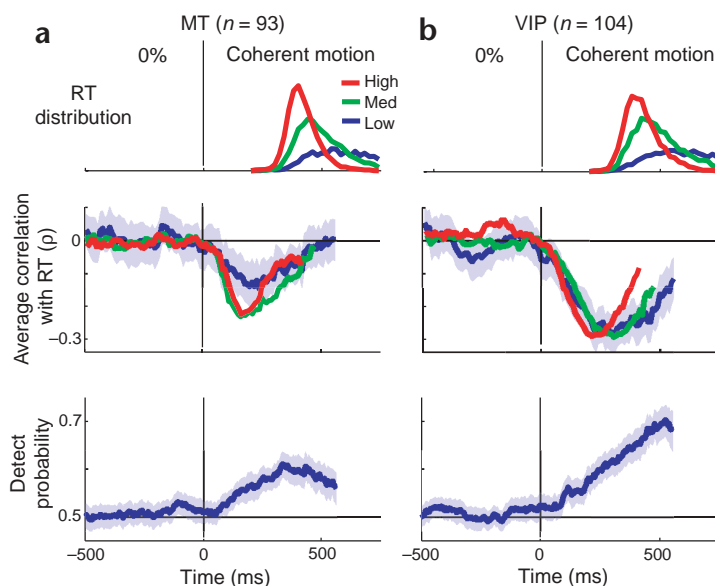


Fig. 3. Average correlation of neuronal responses with RT and detect probability for MT (a) and VIP (b). Top, RT distributions for each level of motion coherence (red high, green medium, and blue low). The vertical lines at time zero correspond to the onset of the coherent motion. Middle, correlation of MT and VIP responses with RT computed for each level of motion coherence and averaged across neurons. Bottom, detect probability averaged across neurons for the low coherence condition for MT and VIP. The 95% confidence interval of the mean for the low coherence condition is shown by the light blue region (bootstrap⁴⁰). Confidence intervals for the medium and high coherence data were approximately the same width as that for the low coherence and not shown for clarity. Each line is terminated at the median RT for its coherence level.



used to describe how neuronal responses vary between two behavioral choices in a discrimination task^{13–15}. It is the probability that an ideal observer could predict the behavioral choice of the animal given the neuronal responses. For our task, the two behavioral outcomes were either correct detection of the coherent motion or the failure to respond. We computed choice probability from our data, but termed the results as detect probability to emphasize that we were using a detection task.

We plotted detect probability as a function of time (Fig. 2b, example MT cell). Only for the low motion coherence condition were there enough missed trials to compute a detect probability. A detect probability of 0.5 before the coherent motion began indicates the neuronal activity corresponding to correct trials was not obviously different than the neuronal activity corresponding to missed trials. After the coherent motion started, detect probability increased, indicating larger neuronal responses were associated with detection of the coherent motion.

Both MT and VIP exhibited strong detect probabilities after the coherent motion began (Fig. 3). Although a small positive trend exists, there was no significant relationship between neuronal responses and detection performance before the coherent motion began.

The magnitude and time course of the detect probability was strikingly different between the two brain regions. MT responses were most predictive of detection performance ~300 ms after the coherent motion began. In contrast, the predictive ability of VIP responses steadily increased throughout most of the RT window and was similar to choice probability measurements from the lateral intraparietal area (LIP)¹⁶. The different dynamics of the covariance between neuronal responses and behavior (as revealed by ρ and detect probability) indicates that MT and VIP may play different roles in the detection of coherent motion.

Effects of attention and stimulus

Although the results in Fig. 3 suggest that variations in the neuronal responses were associated with the animal's behavior, they reveal nothing about the source of this variability. One possibility is that the animal switched spatial attention back and forth between the two patches of dots, which could produce correlations between neuronal responses and behavior. If this occurred, however, either a positive detect probability or negative correlation with RT would be expected before the onset of coherent

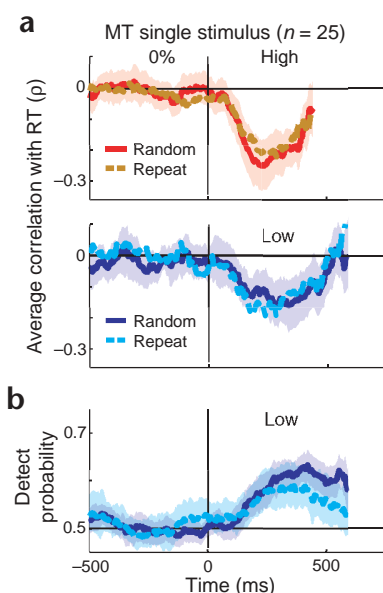


Fig. 4. Average correlation of neuronal responses with RT and detect probability when a single stimulus was presented. (a) Average correlation of neuronal responses with RT. The vertical line at time zero corresponds to the onset of the coherent motion. Solid lines are the random condition where a unique random dot stimulus was presented for every trial. Dashed lines are for the repeat condition where the same random dot motion stimulus was presented on every trial. For clarity, 95% confidence intervals for the mean are shown only for the random stimulus condition (confidence intervals were similar for the repeated stimulus conditions). The two levels of motion coherence used (low and high) were adjusted to produce the same behavioral performance range as in the two-patch design (average behavioral performance across all single patch experiments was 55, 54, 99 and 99% correct for the low random, low repeat, high random and high repeat conditions, respectively). Data are from MT of one monkey, and all other aspects of the motion detection task were the same as that of the two-patch design. (b) Detect probability averaged across neurons for the low-coherence condition for both the random and repeat conditions. Colored regions are the 95% confidence intervals for the means. All lines extend to the median RT.



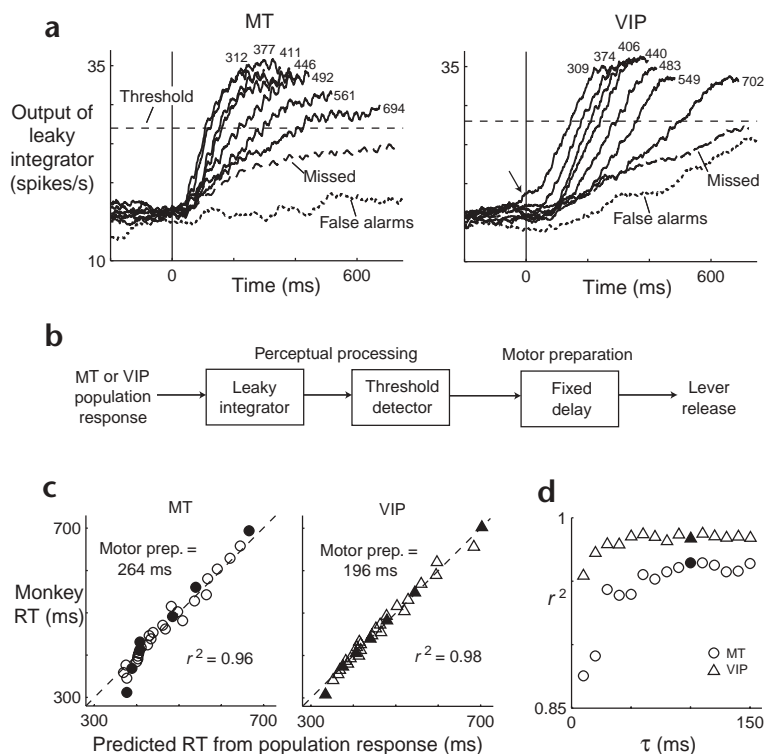


Fig. 5. Population responses of MT and VIP predict RT. **(a)** Responses from all coherence levels were binned by RT and averaged across neurons (solid traces). Thirty RT bins were used, and responses were smoothed with an exponential filter ($\tau = 100$ ms) and aligned to the onset of the coherent motion (vertical line). Every neuron contributed to every RT bin. For clarity, only bins 1, 5, 10, 15, 20, 25 and 30 are shown along with the mean RT associated with each bin. Dashed traces are responses for trials where the monkey failed to release the lever. Responses associated with false alarm trials where the monkey released the lever before the coherent motion began (dotted traces) are aligned with the lever release occurring at $t = 750$ ms. The slight ripple visible in the MT responses is associated with the update rate of the motion stimulus. The horizontal dashed line is the threshold that best accounts for the average RT. **(b)** Threshold detection model. The smoothed neuronal population responses in **(a)** correspond to the output of the leaky integrator. **(c)** Performance of optimized threshold detection model applied to the neuronal population responses. Predicted RT is the time that population responses cross the threshold (shown in **a**) plus the motor preparation delay. Filled symbols correspond to the neuronal responses in **(a)** and dashed lines are unity slope. **(d)** Proportion of variance (r^2) of RT that is accounted for by the threshold detection model using a range of time constants (τ) for the leaky integrator. Filled symbols correspond to the data from **(a and c)** using a $\tau = 100$ ms.

motion, because modulations in spatial attention would produce correlations between neuronal responses and RT (especially in VIP, which had robust attentional modulation)¹². However, we found no systematic relationship between neuronal responses and behavior before the coherent motion onset (Fig. 3).

Another possibility is that the variability in neuronal responses is due to the stochastic nature of the stimulus. The random pattern of moving dots may have produced a weaker motion signal on some trials, which resulted in smaller neuronal responses and longer RTs (or missed trials). To test the contribution of the stochastic stimulus to RT, we presented one monkey with the same set of motion stimuli on two consecutive days. We repeated this experiment using different stimulus locations and found a weak correlation between RTs on the first day versus the second (mean correlation coefficients (r) of 0.2 ± 0.09 , 0.23 ± 0.04 , and 0.16 ± 0.05 for the low, medium, and high coherence, respectively; $n = 8$). Thus, the stochastic variability of the stimulus might explain the covariances between neuronal responses and behavior observed in Fig. 3.

Fig. 6. Neuronal latency of the binned population responses from Fig. 5a versus the average RT associated with each response. Neuronal latency was computed by determining when the population responses during the coherent motion became statistically different from the population responses during the 0% coherent motion. The distribution of population responses that occurred during the 200 ms before the onset of the coherent motion were fit using a normal distribution using maximum likelihood estimation. This normal distribution describes the probability distribution of neuronal responses when no coherent motion was present. The statistical threshold for a response exceeding the 0% coherent baseline was set at $P = 0.001$. Dashed lines are unity slope. The latencies of MT responses are relatively constant, while those of VIP increase with RT.

To control for the effects of both the stochastic stimulus and attention, we had one monkey perform the motion detection task with only a single patch of random dots. This removed any confounds from spatial attention by eliminating any uncertainty of where the coherent motion would occur. To address the effects of the stochastic stimulus, half the trials repeated the same random dot stimulus, and were randomly interleaved with the standard random dot stimulus.

Fig. 4 shows the results from 25 MT neurons. The magnitude and time course for both the neuronal correlation with RT and detect probability in the single-patch experiments are

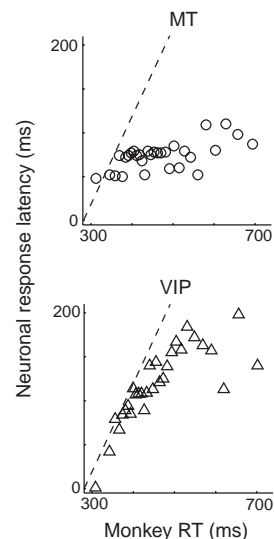
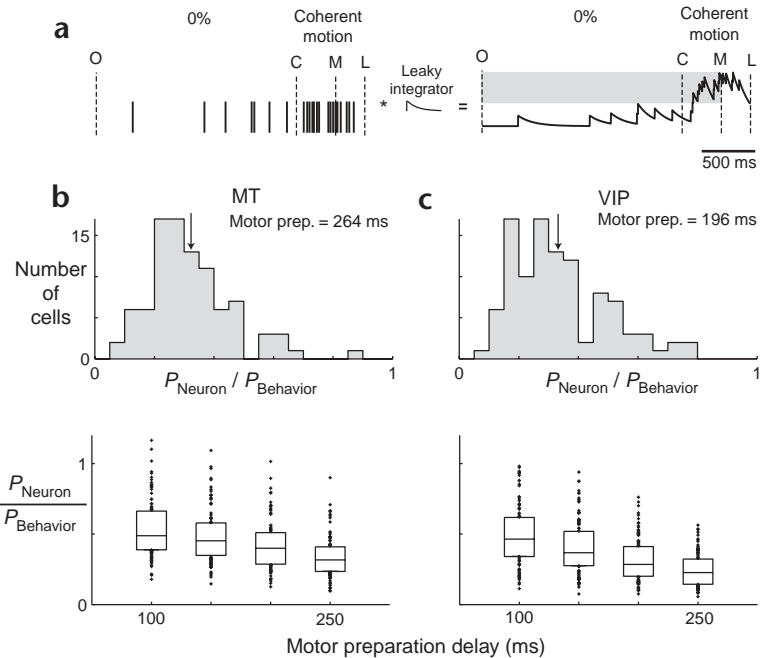


Fig. 7. Single-neuron detection performance.

(a) Applying the neurometric analysis to a high coherence trial from the example MT neuron in Fig. 2. Spike times (left) are convolved with the leaky integrator (middle) to produce the filtered response (right). Onset of 0% coherent motion (O); onset of coherent motion (C); motor preparation delay (M to L); lever release (L). Gray region in right panel is the range of possible thresholds that would allow a threshold model to correctly detect the coherent motion before the beginning of the motor preparation for this particular trial. Lower thresholds would result in the neurometric model incorrectly reporting the coherent motion before it occurred. Higher thresholds would cause the neurometric model to miss the coherent motion. (b, c) Top, the distribution of the ratio of single neuron detection performance (P_{Neuron}) to behavioral detection performance (P_{Behavior}) using motor preparation delays of 264 ms for MT and 196 ms for VIP. P_{Neuron} and P_{Behavior} are the proportion of trials where the coherent motion was correctly detected. Single-neuron performance was optimized across all coherence levels for each neuron individually. Arrows are the medians. Bottom, performance ratio distributions for a range of motor preparation delays. Box plots are median and middle quartiles with outliers plotted individually.



very similar to that of the two-patch data (Fig. 3). Thus, it was unlikely that variability in spatial attention produced the observed covariances between neuronal responses and behavior. Similarly, when the stochastic variability in our stimulus was removed in the repeat condition, there was no appreciable effect on ρ . Although detect probability was reduced, this reduction was not significant ($P = 0.09$ for the average detect probability in the range of 300–600 ms; t -test).

These results agree with previous studies showing that the stochastic variability of random dot motion stimuli does not affect the variability of neuronal responses in MT¹⁷ or the covariation between neuronal activity and behavioral choice¹⁴. This may seem surprising given that repeated presentations of motion stimuli produce consistent patterns of response from trial-to-trial in many MT neurons^{18,19}. However, even the most temporally precise MT neurons we recorded still showed some variability in response to identical stimulus presentations. The source of this variability is unknown.

The analyses in Figs. 3 and 4 provide two measures of the relationship between neuronal responses and behavior. The peaks in the RT correlation analysis suggest that neuronal activity was most predictive of behavior 200–300 ms after the coherent motion began. By the median RT, the average ρ was substantially reduced. Thus, neuronal activity covaries with RT over a limited time window after the start of the coherent motion. Detect probability, in contrast, peaks later and is more sustained (and may be more sensitive to the elimination of stimulus variability, Fig. 4b). To understand the reason for these differences, as well as the different roles these two brain areas may have during motion detection, we next examined the neuronal population responses.

Dynamics of the neuronal population responses

How do the monkeys use the neuronal responses from MT and VIP to generate their behavioral report of the coherent motion?

RT correlation and detect probability do not provide enough information to identify specific features of the neuronal response that varied with RT and detection performance. For example, either a variable rate of rise or a variable latency in the neuronal response could produce the negative RT correlations. Another important feature that has not been clearly defined is the temporal window the animals used to integrate the neuronal signals during the task. It is likely, however, that the monkeys based their detection on the average activity of a population of neurons. If this were the case, then combining responses from many neurons for a given RT should reveal the features of the neuronal responses that underlie the decision to release the lever.

To investigate how MT and VIP population responses vary with RT, we first sorted responses from all three motion coherences based on RT (all the results to follow are from the two-patch experimental design). The sorted responses were uniformly distributed across 30 RT bins (Fig. 5a). The population responses binned on RT vary in an orderly manner for both MT and VIP and suggest that the animals used a fixed threshold to detect the onset of the coherent motion. Threshold-detection models have been used to relate neuronal activity and behavioral performance during RT tasks^{20,21}. Fig. 5b shows such a model of the detection process that has two parts: a perceptual processing stage where the stimulus is detected, and a motor preparation stage that produces the lever release²².

Models that convert neuronal activity in visual cortex to behavioral performance have traditionally held the premise that the brain integrates spikes over the entire stimulus period. While these models can be applied to behavioral tasks that use fixed intervals of stimulus presentation, they are not suitable for detection tasks where the onset time of the stimulus is unknown. An alternative is to use a leaky integrator to integrate spikes from MT and VIP. The exponential smoothing filter used above is essentially a leaky integrator. Thus, our model



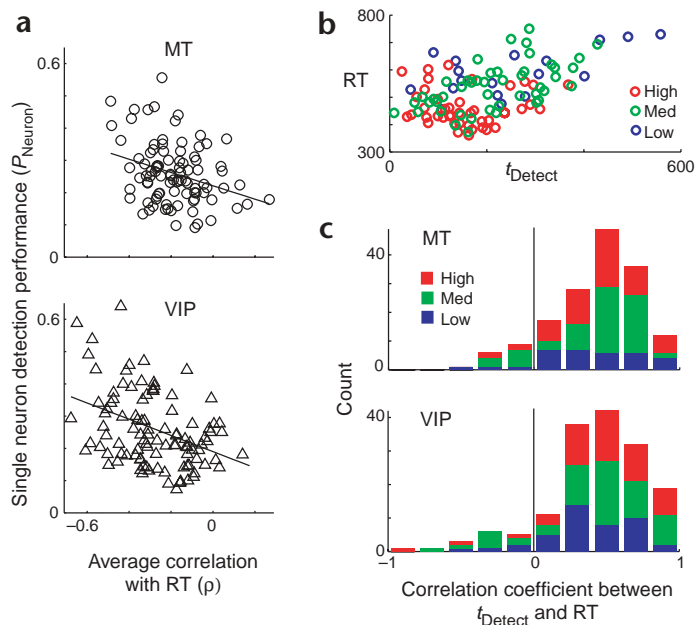


Fig. 8. Comparison of single-neuron detection performance with RT. (a) Single-neuron detection performance versus average RT correlation for MT and VIP. Average RT correlation was computed by averaging ρ across all three motion coherences using a 50-ms window that approximately corresponded to the peak correlations in Fig. 3. Windows started at 170 and 230 ms after the coherent motion began for MT and VIP, respectively. Single neuron detection performance is from Fig. 7 using motor preparation delays of 264 and 196 ms for MT and VIP. Regression lines are shown (MT, $r = 0.31$, $P = 0.002$; VIP, $r = 0.40$, $P < 0.001$, F -test for slope = 0). (b) Monkey RT versus the neuron's detection time (t_{Detect}) for the example MT neuron in Fig. 2. Only trials in which both the animal and the neuron correctly detected the coherent motion were used, and t_{Detect} is the time the neuronal response crossed the optimized threshold as determined using the neurometric analysis in Fig. 7. (c) Distribution of the correlation coefficients between RT and single neuron neurometric detection time for MT and VIP.

assumes that the output of the exponential smoothing filter is the signal that the monkeys used to make their decision to release the lever. Once this signal crosses the threshold, the lever is released after a fixed motor preparation time. The model assumes the variability in RT is due only to the perceptual processing stage.

We optimized the threshold and motor preparation delay to provide the best match between actual RT and predicted RT for MT and VIP separately. The optimized thresholds are shown in Fig. 5a and the optimized motor preparation time was 264 and 196 ms for MT and VIP. A shorter motor preparation time for VIP is consistent with its anatomical location later in cortical processing²³. Using the optimized parameters, we plotted the predicted RT from the neuronal population responses against the actual average RT for each bin (Fig. 5c). The neuronal population responses from MT and VIP varied systematically with RT in a way that allows a threshold model to accurately predict behavior. The time the population responses cross threshold (Fig. 5a) roughly corresponds to the peaks in the RT correlation plots (Fig. 3).

The neuronal population responses also account for the detect probability time course. On average, trials in which the monkeys failed to release the lever did not cross the threshold. This was the case for both MT and VIP and is shown by plotting the average response to the missed trials. The time course of the missed responses (Fig. 5a) is consistent with the detect probability time course (Fig. 3). The separation between responses to missed trials and correct trials slowly increased, and for VIP, became larger throughout most of the coherent motion.

These results were not sensitive to the parameters used to integrate the neuronal responses. In Fig. 5d, the proportion of RT variance accounted for by the population responses (r^2) is shown for a range of integrator time constants (τ). Even for short τ , the neuronal population responses predicted average RT. We also found that the ability of the neuronal population responses to predict RT was not sensitive to the shape of the integrator. For example, an integrator modeled as a 100-ms square pulse

resulted in $r^2 = 0.90$ and 0.97 for MT and VIP, respectively. In addition, we found the same relationship between neuronal population responses and behavior when data from each animal were analyzed separately.

VIP responses contain a non-sensory component

Neurons in LIP show responses that can provide information about a monkey's decision before a stimulus is presented²⁴. For VIP, which is anatomically adjacent to LIP, responses associated with the fastest RT bins were elevated before the coherent motion began (arrow in Fig. 5a). It is possible that for the fastest RTs, the monkeys may have been biased to release the lever before the coherent motion began and that a signal of this bias may be reflected by the early rise of the VIP responses. Event-related potentials recorded in human subjects during RT tasks have demonstrated motor preparation signals that begin before the sensory signals on the fastest RT trials²⁵. Thus, VIP responses may contain an efferent feedback signal reflecting the monkey's plan to release the lever.

Additional evidence for a non-sensory signal in VIP responses can be found in trials where the monkeys released the lever before the coherent motion began (false alarms). There was little increase in the MT response before lever release, as would be expected for a sensory region of visual cortex (Fig. 5a). In contrast, VIP showed a substantial increase in the response before the lever was released, even though no coherent motion was present.

Neuronal latency versus RT

The rising edge of the neuronal population responses is a feature that correlates well with behavior. We found, however, that the latency of the rise in neuronal activity differed between MT and VIP (Fig. 6). In MT, there was only a modest increase in latency as a function of RT; in VIP, neuronal latencies increased almost linearly with RT. The latencies for MT were similar to those from previous studies^{26,27}. From Fig. 5a it is evident that MT responses had a relatively constant latency for response onset, but their rate of rise varied. By comparison, VIP responses had a variable latency, but similar rates of rise (except for the longest RTs). On this basis, VIP responses were more 'motor-like' than MT responses.

Motion detection capability of individual neurons

The population analysis suggests that the average response from either MT or VIP accounts for much of a subject's ability to detect

the coherent motion. This analysis, however, does not tell us how reliable individual neurons were at reporting the coherent motion. Because we now have an estimate of the time window the animals used to detect the coherent motion (from the motor preparation delay in Fig. 5), we can address the signaling capabilities of MT and VIP neurons using the same realistic detection times.

We computed the ability of single neurons to detect the presence of coherent motion using the same threshold model outlined in Fig. 5b. An example of this neurometric analysis is shown in Fig. 7a for a high-coherence trial taken from the representative MT neuron. On the left in Fig. 7a is a single trial showing the time of each action potential, and the right panel shows the same data after the spike train has been convolved with the leaky integrator ($\tau = 100$ ms). We limited the duration of the responses to the coherent motion using the estimate of the motor preparation delay for MT. The point marked "M" is 264 ms before the response time, and spikes occurring after this time were not used. Thus, the neurometric analysis only used the portion of the neuronal response used by the monkey in making its response.

A range of thresholds could be set for this particular trial to give a correct detection of the coherent motion (Fig. 7a, right). As we did not know what threshold the monkey used, we optimized the threshold to maximize the number of correct detections for each individual neuron across all three levels of coherent motion. Although the neuron did a good job of signaling the occurrence of the coherent motion on this particular trial, individual neurons were poor detectors of coherent motion compared to the monkeys. We computed the distribution of the ratio of the neuron's detection performance (P_{Neuron}) to the monkey's detection performance (P_{Behavior}) for each cell (Fig. 7b and c). For the representative MT neuron in Fig. 2, the monkey correctly detected the coherent motion signal on 85% of the trials; the neurometric model detected the coherent motion on 33% of trials ($P_{\text{Neuron}}/P_{\text{Behavior}} = 0.39$). No individual MT or VIP neuron had a detection performance equal to or better than the monkey's.

The length and shape of the integration window had little effect on the capabilities of individual neurons, although for very short integration windows ($\tau < 25$ ms), neuronal performance was reduced. The motor preparation delay had a much bigger impact on neuronal performance because it limited the period of the neuronal response that could be used. The ratio of detection performance over a range of motor preparation delays (Fig. 7b and c, bottom) shows that the capabilities of individual neurons improve as the motor preparation delay becomes smaller. This is because a smaller motor delay ($M \rightarrow L$ in Fig. 7a) provided the neurometric analysis with more spikes during the coherent motion. In contrast to most previous comparisons of neuronal and behavioral performance that used longer periods of response, the median neuronal detection performance was always much less than the animal's detection performance. This was observed for all motor preparation delays and all integration window sizes and shapes examined. In addition, similarly poor neuronal performance was also found for the MT responses recorded in the single-patch experimental design.

Single neuron detection covaries with RT

So far, we have assessed how well single neurons are correlated with RT and how reliable they are at signaling the onset of the coherent motion. How are these two aspects of single neuronal activity related? We plotted the single-neuron detection performance against the average peak RT correlation for each neuron (Fig. 8a). Neurons that were more reliable at indicating the onset of the coherent motion were also better correlated with RT. This

result is similar to other studies that examine choice probability^{13,14} and suggests that the monkeys based their decision of when to release the lever on neurons that provided the most reliable signals regarding the coherent motion.

We asked if the time a single neuron detected the coherent motion (using the neurometric analysis above) was related to the animal's RT on a trial-by-trial basis. For the example MT neuron in Fig. 2, we plotted monkey RT against the neurometric detection time (t_{Detect}) for each level of motion coherence (Fig. 8b). For this neuron, the time the neurometric analysis detected the coherent motion was weakly correlated with RT for the low and medium, but not the high, coherence levels.

The distribution of the correlation coefficients between t_{Detect} and RT computed for each level of coherence separately is shown in Fig. 8c for neurons in MT and VIP. Although there is a large amount of scatter, longer behavioral RTs were consistently associated with longer single neuron detection times. Although the neurometric analysis suggests that single neurons are not reliable detectors of the coherent motion when realistic processing times are used, the correlation between RT and t_{Detect} adds further evidence that perceptual performance was based on the rising edge of neuronal activity.

DISCUSSION

Detection capability of single neurons

That single neurons had substantially worse detection capabilities than the monkeys did stands in contrast to most previous studies. For example, in a similarly designed study⁴, it was found that many MT neurons exceed the monkey's discrimination capabilities. One possible explanation for the different results is that MT neurons are used for direction discrimination, but are less well suited for the motion detection task used here. However, thresholds of MT neurons are at least as good for detection as they are for discrimination. In addition, both the trial-by-trial correlation of neuronal responses with RT and detection performance suggest that these areas were probably involved in the detection process.

Several differences in the analysis may have contributed to the different results. First, the earlier study used a model of motion discrimination that compared two neurons with opposite preferred directions of motion sensitivity. Those results, therefore, are based on the activity of two neurons, whereas our estimate of the motion detection capability is based on the output of single neurons. However, neurometric performance would only increase if the neurons were inhibited for motion in the null direction. Second, the previous study reports that the shape of the average neurometric function matches the shape of the monkeys average psychometric function. The slope of the neurometric function from our data did not match the slope of the animals psychometric function. The slope of our neurometric function could be made more similar to the monkey's psychometric slope only if thresholds were raised, which reduced single-neuron performance. Thus, our single-neuron performance is an upper bound. Third, because some of our stimuli were well above threshold, the animals may have been monitoring a larger pool of neurons which included those with lower detection performance. However, the relationship between neuron detection performance and the correlation with RT (Fig. 8a) suggests the animals' behavior was based on the activity of neurons that were more reliable indicators of the coherent motion.

A more likely reason for the different outcomes is the different time periods used in each analysis. The duration of the neuronal activity in response to the coherent motion in our analysis

was relatively short compared to other studies. This is important because the variability of estimates of neuronal response (such as spike count) increase when computed over shorter intervals of time. The neuronal detection performance increased as the motor preparation interval was reduced (Fig. 7). The duration of neuronal activity used in our analysis, however, was always bound by the monkey's RT. The previous study used a fixed interval task in which the animals observed the random dot motion stimulus for two seconds before making their report. The long fixed viewing interval makes it difficult to estimate the duration of the perceptual processing stage. When the authors reduced the stimulus interval, they reported that both neuronal and behavioral performance decreased. However, it was not indicated whether neurons would have had better performance than the animals at stimulus durations comparable to those used here. Recent studies suggest that subjects in a fixed interval motion discrimination task may not use the entire stimulus period to make their behavioral decision (J. D. Roitman & M. N. Shadlen, *Soc. Neurosci. Abstr.* 24, 106.5, 1998).

Most studies that have simultaneously measured neuronal activity and perceptual performance have used task designs where the behavioral report was delayed in time from the stimulus presentation period. This may have led to an overestimation of the amount of neuronal activity the subjects used to perform the task, which would artificially increase the estimated signaling capabilities of individual neurons.

Covariance of neuronal responses and behavior

The average detect probability for MT in our motion detection study was slightly higher than choice probabilities previously observed using a motion discrimination task¹⁴, although higher MT choice probability has been reported using a stereoscopic depth discrimination task¹⁵. The detect probability for VIP, however, was similar in magnitude and time course to choice probability observed in LIP²⁴. The similar detect probabilities that we found are surprising given the fact that we used weighted spike counts over a relatively short window (as determined by our exponential filter). The spike counts over the much longer windows used in the other studies would be expected to produce higher detect/choice probabilities because longer windows yield less variability in estimates of neuronal responses. It is possible that detect probability was enhanced in our task because the animals based their decisions on a relatively short period of spike activity.

Perceptual processing accounts for RT variability

It has previously been reported¹¹ that the neuronal latency of visual responses in FEF has no relationship to the latency of saccades, suggesting that RT variability is mainly determined by the motor preparation stage. In contrast, the correlation between neuronal responses and RT that we found in both MT and VIP suggests that RT variability is due in part to the perceptual processing stage. Because of the differences in the tasks and recording locations, a direct comparison between data from the two experiments is difficult. One possibility, however, is that unlike the FEF study, we recorded directly from visual cortex using stimuli matched to the response properties of the neurons and thus increased the probability of observing correlations between neuronal responses and RT.

The results of the population model (Fig. 5) suggest that almost all the variability in RT can be accounted for by averaging the activity of many neurons in either MT or VIP. One might interpret this to mean that processing after MT and VIP adds little additional variability. We do not think this is the case, however, because

it is possible that by binning responses on RT, we may have diminished the effect of variability in the motor preparation stage. The population model assumed that averaging responses with similar RTs from neurons recorded on different days (and different animals) was equivalent to averaging across the neurons that simultaneously contributed to the behavior on a single trial. We do not know how neuronal responses are combined in the brain on a single trial. This is especially important when one includes factors such as correlated noise that reduce the effects of averaging^{28–30}. Neither do we know the number of neurons that contribute to the monkey's motion detection. Nevertheless, it is highly unlikely that the orderly temporal separation of neuronal responses (Fig. 5) would have occurred if the rising phase of the population response did not account for some fraction of the variability in RT. The trial-by-trial correlation between neuronal response and RT further supports this conclusion.

How realistic are the motor preparation delays of 264 and 196 ms for MT and VIP (Fig. 5)? During a simple RT task, activity of neurons in motor cortex occurs an average of 122 ms before movement begins³¹. Thus, much of the motor preparation time we computed may be due to the execution of the motor command to release the lever (which would also entail the delay produced by the mechanism of the lever).

Our results are in good agreement with models of RT that accumulate sensory information until a threshold is reached^{10,20,21,32}. One difference, however, is that we found the accumulator could be modeled as a leaky integrator that gives more weight to recent sensory information³³. As long as the time constant was greater than ~25 ms, the results were not qualitatively sensitive to the duration and shape of the leaky integrator. Shorter integration windows fail because they allow too much high frequency noise to get through. However, it is possible to counteract this effect by including the responses of more neurons. Thus, it is possible very little accumulation of sensory information was performed by the monkeys if they could sample many more neurons than we had in our analysis. A short integration window would reduce the perceptual processing stage and lengthen the response preparation period by increasing the rate of rise of the integrated MT and VIP responses.

Source of the covariance between neurons and RT

We have demonstrated that neuronal responses in MT and VIP covary with the time it takes a subject to detect a motion stimulus. What is the source of this covariation? Although we had not set out to answer this specific question, this study allows us to at least address several possible contributions. The results of the control experiment using a single patch with identical stimuli (Fig. 4) suggests that spatial attention did not contribute much to the covariation between neuronal response and behavior. They similarly show that the stochastic nature of the stimulus was not a major factor. The reduced detect probability when stimulus variability was eliminated, while not significant, suggests that the stochastic nature of the random dots contributed a small component to the covariation. Although no effect was seen on the correlation between neuronal response and reaction time, it is possible that a less detectable effect exists there as well, but probabilistic aspects of the stimulus were not a substantial part of either relationship between neuronal response and behavior.

In addition, we found that variability in the animal's vigilance as a function of time did not contribute to this covariation as neither neuronal response nor RT were correlated with the time the coherent motion started within a trial (average correlation coefficients were between -0.01 and 0.01 for both MT and VIP).

During a trial, the monkey's eye position varied within the fixation window. We found no relationship between neuronal responses and eye position (or eye speed) in either MT or VIP (average correlation coefficient, ~ -0.03), and thus it is unlikely eye position introduced the correlations shown in Fig. 3. There was a weak relationship between eye position/speed and RT that peaked after the coherent motion began (average peak correlation coefficient, ~ 0.15). The animals had faster RTs when fixation was closer to the stimulus. This effect was small, however, with the average difference in eye position for slow and fast RTs less than 0.05° . One possible explanation for these results is that fixating closer to the stimulus may produce an enhanced representation of the motion stimulus in visual cortex, owing to greater magnification of more central parts of the visual field, and therefore support faster RTs. An individual neuron's response, however, is a function of the overlap of the RF and stimulus. This overlap would not be consistently improved by fixation close to the stimulus, so no correlation would be seen between eye position and the responses of individual neurons.

The role of MT and VIP

The responses of MT and VIP differ in ways that suggest they perform different roles in our task. MT is likely to be the first area in the visual cortical hierarchy that would provide the monkey with the kind of motion information needed for this task. By comparison, VIP has more complex response properties. It receives a strong input from MT³⁴ with many neurons exhibiting directional selectivity³⁵. VIP neurons also show large spatially directed attentional modulation¹². The increase in neuronal activity during the false alarm trials indicates that VIP responses contain both a visual and extra-retinal component that may reflect integration of sensory information with the decision process. This type of input to VIP would explain why VIP responses showed slightly better correlation with behavior than MT in all of our analyses. A full understanding of the role of VIP responses in this task, however, will require further investigation.

METHODS

Behavioral task. All procedures were done in compliance with standards of the Baylor College of Medicine Animal Research Committee. Two monkeys (*Macaca mulatta*) were trained to perform a spatially cued motion detection task (Fig. 1). At the beginning of each trial, a static cue was presented, indicating which patch of dots would contain the coherent motion. The purpose of the static cue was to direct the attention of the monkey to either patch. In 20% of the trials, the coherent motion signal occurred in the uncued patch. However, only trials where the cue and the coherent motion both appeared in the RF of the neuron were used in our analyses.

For the control experiments in Fig. 4, a single patch of random dot motion was presented in the neuron's RF. Trials that used the same dynamic random dot stimulus were interleaved with those that were randomly seeded. For the repeated condition, one long movie was constructed and each trial began at a different a time point depending on when the coherent motion was to begin.

The monkey received a reward only for correctly releasing the lever within the RT window. Failures to release the lever or early releases were not rewarded. Trials during which fixation was not maintained within 1° of the fixation point were aborted and not analyzed. The two patch experiments were run in a block mode in which the cue was presented at the same location for 15 completed trials.

Visual stimuli. The strength of the coherent motion was varied randomly on each trial among four preset values: three levels of non-zero coherence (low, medium and high) and 0% coherent catch trials for the two-patch experiments. The single-patch experiments used two levels of coherent motion (low and high). The values of the non-zero motion

coherence were adjusted for each stimulus configuration to produce a range of behavioral performances for the animal.

The animals sat 62 cm from a computer monitor ($\pm 17 \times \pm 13$ degrees of visual angle, $1,600 \times 1,200$ pixels, 75-Hz refresh). The stimuli consisted of two patches of white dots (each 0.25° in diameter, 78 cd/m^2) on a dark gray background (12 cd/m^2) with a dot density of 2.1 dots/deg². Each patch of dots was updated every other frame (37.5 Hz). A complete description of how the random dot stimuli were generated is reported elsewhere¹².

Neuronal recording and data collection. Standard extracellular recording techniques³⁶ were used to record neurons. The location and size of the RF and preferred speed of each neuron were determined manually using a moving bar. The directional tuning of the neuron was determined using the motion detection task described above with motion presented in eight directions¹². The number of completed trials per coherence level for the motion detection task ranged from 15 to 175 (median 35). For the single-patch control experiments, this range was 40–234 (median 102) completed trials. The monkey's performance varied with patch location, size and motion speed, which were determined by the response properties of the neuron under study. Consequently, different neurons were tested with different coherence levels. The animal's eye position was measured every 5 ms using a scleral search coil^{37,38}, and action potentials were recorded with a precision of 1 ms.

A total of 102 MT cells and 104 VIP cells were recorded from the two animals. Histological reconstruction of the recording sites was made only for Monkey 1. The extent of MT was mapped using myelin-stained sections³⁹. Of 56 neurons recorded in the superior temporal sulcus in Monkey 1, nine were not unequivocally within MT and were excluded from analysis. Sections of the intraparietal cortex revealed that we recorded from neurons located in the ventral portion of the lateral bank. Recordings from the lateral bank of the intraparietal sulcus were within 3 mm of the fundus, which has been identified as VIP³⁵. The Horsely-Clark coordinates of the MT recordings ranged from 4–7 mm posterior and 15–18 mm lateral. The VIP coordinates ranged from 1 mm posterior to 2 mm anterior, and 10–14 mm lateral.

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Competing interests statement

The authors declare that they have no competing financial interests.

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