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Context-Dependent Changes in Functional Circuitry in Visual Area MT

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SUMMARY

Animals can flexibly change their behavior in response to a particular sensory stimulus; the mapping between sensory and motor representations in the brain must therefore be flexible as well. Changes in the correlated firing of pairs of neurons may provide a metric of changes in functional circuitry during behavior. We studied dynamic changes in functional circuitry by analyzing the noise correlations of simultaneously recorded MT neurons in two behavioral contexts: one that promotes cooperative interactions between the two neurons and another that promotes competitive interactions. We found that identical visual stimuli give rise to differences in noise correlation in the two contexts, suggesting that MT neurons receive inputs of central origin whose strength changes with the task structure. The data are consistent with a mixed feature-based attentional strategy model in which the animal sometimes alternates attention between opposite directions of motion and sometimes attends to the two directions simultaneously.

INTRODUCTION

The appropriate behavioral response to a given sensory stimulus depends greatly on context. For example, whether a person chooses to answer a ringing telephone depends on whether that person is at home or is a guest in someone else's home. This simple example is only one of many ways the mapping between stimulus and response can depend on context. Well-trained monkeys are capable of learning large numbers of arbitrary associations between particular sensory stimuli and behavioral actions (for review, see Wise and Murray, 2000). New associations can be learned within several tens of trials, and switching between learned associations can occur in as little as a single or a few trials in response to explicit task cues or to changes in reward contingencies (di Pellegrino and Wise, 1993; Boussaoud et al., 1995; Wise et al., 1996; Asaad et al., 1998, 2000; Murray et al., 2000; Miller et al., 2003; Wallis and Miller, 2003; Muhammad et al., 2006; Kennerley et al., 2006).

Context-dependent behavior of this nature directly implies the existence of context-dependent mapping between sensory representations in the brain and the neural circuits that control behavior. Furthermore, the functional connectivity underlying learned sensorimotor associations must be capable of very rapid modification in order to mediate rapid behavioral switching between associations (Salinas, 2004a, 2004b). Prior electrophysiological studies have shown that changes in functional connectivity within a circuit can be inferred from measurements of correlated discharge among simultaneously recorded neurons. Such changes in neural circuitry can be induced in sensory areas by changes in stimuli (Espinosa and Gerstein, 1988; Aertsen et al., 1989; Ahissar et al., 1992a) and by learning (Ahissar et al., 1992b), and in frontal cortex by changes in behavioral context (Vaadia et al., 1995). Consistent with the modeling studies (Salinas, 2004a, 2004b), the observed changes in correlation structure can be very rapid, occurring at timescales substantially less than the duration of typical behavioral trials (Ahissar et al., 1992b; Vaadia et al., 1995).

The goal of our study was to detect dynamic changes in functional connectivity within visual cortex during performance of a task in which the appropriate behavioral response to a particular visual stimulus changed on a trial-to-trial basis. We studied changes in functional circuitry between direction-selective neurons in the middle temporal area (MT) while monkeys performed a version of a two-alternative forced-choice (2AFC) direction discrimination task (Newsome and Pare, 1988; Newsome et al., 1989; Britten et al., 1992; Roitman and Shadlen, 2002). Our experimental strategy was to create a situation in which the monkey viewed an identical visual stimulus in two behavioral contexts, and then determine using physiological measurements whether context influences functional circuitry within MT. Specifically, we measured changes in "noise correlation"—the correlation of trial-to-trial fluctuations of visual responses to a given visual stimulus—to infer changes in common input to the two neurons under study.

We analyzed noise correlation while monkeys performed the direction discrimination task in two spatial configurations: one that promotes cooperative interactions between the two neurons under study and another that promotes competitive interactions. We found that noise correlation indeed changes in these two contexts, even when the visual stimulus itself is identical in the two contexts. In addition, we observed that the sign of this context-dependent change in correlation depended on the similarity in the direction tuning of the two neurons.

These results suggest that MT neurons receive inputs of central origin whose strength changes based on the task structure. Furthermore, the physiological data place important constraints on models of the functional circuit involved in this task and how the circuit changes based on task condition. In simulations, we

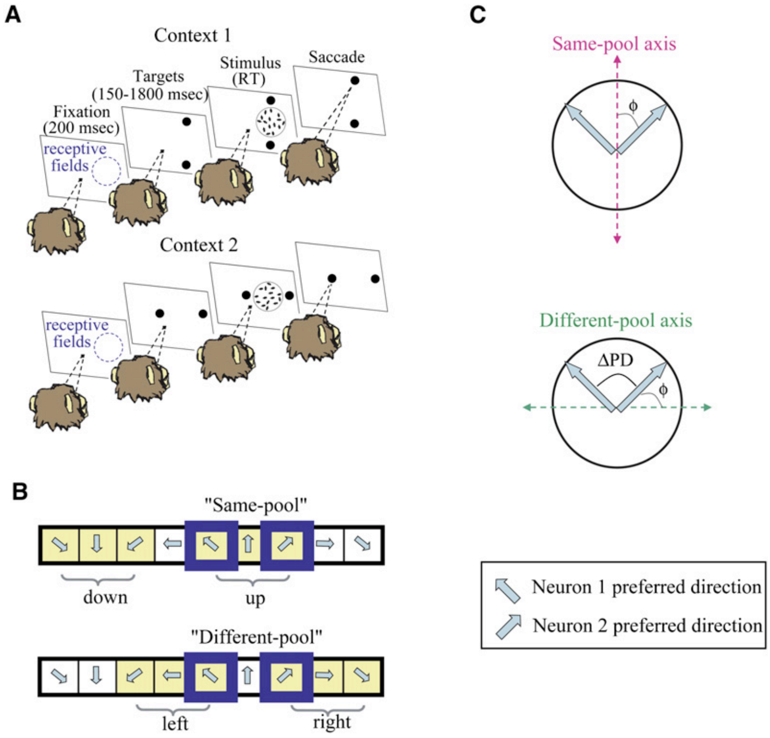

Figure 1. Behavioral Task and Experimental Strategy

(A) Schematic of the behavioral task. We record from pairs of well-isolated single MT neurons whose receptive fields are largely overlapping (first panel, blue dotted line). A trial begins when the monkey fixates a central spot of light (first panel, fixation period). After 200 ms, two saccade targets appear, the position of which indicates the direction of motion to be discriminated on the upcoming trial (second panel, target period). Two orthogonal axes of motion are randomly interleaved from trial to trial (top and bottom). After a random period of time, the stimulus appears in the union of the neurons' receptive fields (third panel, stimulus period). The monkey is free to indicate his direction judgment with a saccade to the appropriate target at any point after the stimulus appears. The stimulus and fixation point disappear as soon as his eyes leave the fixation window (fourth panel).

(B) Schematic of MT direction columns. (Top panel) Same-pool condition. Blue squares indicate the preferred directions of two hypothetical neurons under study. When the monkey performs an up-down discrimination task, the two neurons both contribute to the pool of neurons indicating upward motion (yellow shaded region). (Bottom panel) Different-pool condition. When the monkey performs a left-right discrimination task, the same two neurons contribute to opposite pools; one neuron contributes to the pool indicating leftward motion (first shaded region) while the other neuron contributes to the pool of rightward preferring neurons.

(C) Selection of motion axes. We defined the axis of motion for the same-pool condition (magenta dashed line, top panel) as the axis that bisected the angle between the preferred directions of the two neurons under study (light blue arrows). The different-pool condition axis (green dashed line, bottom panel) was orthogonal to the same-pool axis. We refer to the angle between the preferred directions of the neurons under study as ΔPD and the difference between a neuron's preferred direction and the axis of motion being discriminated as ϕ.

found that a process similar to feature-based attention can account for the pattern of noise correlation changes we observed. In particular, our results are consistent with an attentional strategy in which the animal sometimes alternates attention between two opposite directions of motion and sometimes attends to both relevant motion directions simultaneously.

RESULTS

Experimental Strategy and Behavior

We trained two monkeys to perform a reaction-time version of a 2AFC motion direction discrimination task in which monkeys chose between two opposite directions of motion in a stochastic random dot display (Newsome and Pare, 1988; Newsome et al., 1989; Roitman and Shadlen, 2002). We varied motion strength, and therefore the difficulty of the task, by changing the probability that on a given frame, a given dot was replotted in apparent motion in one of two opposite directions (''percent coherence'').

We manipulated behavioral context by changing randomly from trial to trial the axis of motion that the monkey was required to discriminate. Figure 1A shows a schematic of the behavioral task. A trial began when the monkey fixated a central spot of light (''fixation period''), and then two saccade targets appeared (''target period''). The location of the saccade targets indicated to the monkey which of two orthogonal axes of motion, corresponding to the two behavioral contexts, he was to discriminate (Figure 1A, top and bottom panels). The length of the target period was drawn from a truncated exponential distribution so that the monkey could not anticipate the onset of the motion stimulus. The motion stimulus then appeared (''stimulus period'') within the joint receptive field of the MT neurons under study. Following onset of the visual stimulus, the monkey was free to indicate his direction choice at any time by making a saccadic eye movement to one of the two targets flanking the stimulus.

We selected the two axes of motion such that, in one context, the responses of the two neurons under study were expected to contribute to the same perceptual decision and, in the other context, the two responses were expected to contribute to opposite perceptual decisions. Figure 1B depicts schematically a set of direction columns in MT for a given visual field location, with the arrows indicating the preferred direction of neurons in each column. Consider two neurons, one from each of the bold-outlined columns in Figure 1B. In the context of an up-down discrimination task (Figure 1B, top), these two neurons should contribute to the same perceptual judgment because increases in the firing rate of either neuron should indicate upward motion, and decreases should indicate downward motion. (Evidence from electrophysiological recordings [Britten et al., 1996; Purushothaman and Bradley, 2005] and microstimulation experiments [Nichols and Newsome, 2002] suggests that MT neurons contribute information to decisions in direction discrimination tasks, even when the axis of motion being discriminated is quite different from the preferred direction of the MT neuron.) In contrast, if the monkey performs a left-right discrimination task, the two neurons should act competitively (Figure 1B, bottom); a high firing rate from neuron 1 indicates leftward motion while

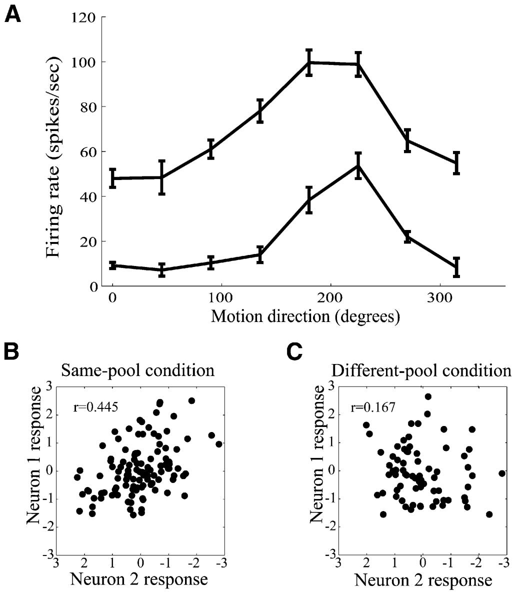

Figure 2. Correlation Results for an Example Pair of Neurons

(A) Tuning curves for each example neuron. Mean firing rate (spikes/s) is shown for eight directions of motion (500 ms stimulus presentations). Error bars represent the standard error of the mean (five to eight presentations of each motion direction). The difference between preferred directions (ΔPD) for this pair was 20°.

(B) Scatter plot of firing rate Z scores for 0% coherence trials (see Experimental Procedures) for neuron 1 (y axis) versus neuron 2 (x axis) in the same-pool condition (113 trials). The trial-to-trial fluctuations in firing rate were correlated, and the correlation coefficient was 0.445.

(C) Same axes and neurons as (B), in the different-pools condition (121 trials). The correlation coefficient here was 0.167.

a high firing rate from neuron 2 indicates rightward motion. Throughout this paper we will refer to the first context as the "same-pool" condition, indicating that the two neurons contribute to a single pool of neurons that drive motion judgments in a particular direction (e.g., upward in Figure 1B). We will refer to the second context as the "different-pool" condition, indicating that the two neurons contribute to different pools, driving opposite judgments (e.g., right and left in Figure 1B).

Our central experimental hypothesis was that the segregation of MT neurons into signaling pools is likely to involve activation of a context-dependent signal that provides, for example, common excitatory and/or mutually inhibitory inputs within or between pools. If this hypothesis is correct, functional inputs to the two MT neurons under study should be different in our two task conditions, and we therefore expected to observe context-dependent changes in noise correlation.

We recorded from pairs of well-isolated, single MT neurons on two electrodes. Upon isolating a pair of MT neurons, we first determined their preferred directions by measuring direction tuning curves during a fixation task (see Experimental Procedures). The preferred directions of the neurons under study determined the axes of motion that corresponded to the same or different-pool conditions. We defined the same-pool condition to be discrimination along the axis of motion that bisected the angle between the two neurons' preferred directions (dotted magenta line in Figure 1C, top). The different-pool condition was the axis orthogonal to the same-pool axis (dotted green line in Figure 1C, bottom).

Note that the way we selected axes of motion for discrimination ensured that in both conditions, the two neurons' preferred directions were equidistant from the axis of motion being discriminated. Furthermore, pairs of neurons with very similar preferred directions will be better suited to discrimination along the axis in the same-pool condition because the preferred directions of both neurons will be close to the motion axis in the same-pool condition, while pairs of neurons with very different preferred directions will be better suited to the different-pool condition. We will refer to the angle between the preferred directions of the neurons under study as ΔPD and the angle between a neuron's preferred direction and the axis of motion being discriminated as ϕ (see Figure 1C). We recorded from pairs encompassing nearly the full range of ΔPDs (minimum 3°, maximum 178°).

For our physiological results to be meaningful, it was essential that the monkey work hard to discriminate the motion signal on each trial. If the monkey simply guessed, we would have no basis for believing that choices were based on MT activity, and thus no basis to expect behavioral context to influence MT firing rates. We therefore only included experimental sessions in which the monkey achieved greater than 90% correct at the highest coherence. By this criterion, we rejected 1/51 datasets (1.96%) for Monkey T and 3/28 datasets (10.7%) for Monkey D.

Noise Correlation during Active Decision Making

Our most important physiological measurement was to compare noise correlation in the two behavioral contexts while the monkey was engaged in deciding the direction of motion of the stimulus. Importantly, we only analyzed data for the 0% coherence condition. On average, therefore, the motion stimuli in the neurons' classical receptive fields were identical in the two conditions; average differences in noise correlation could only be attributed to the task condition.

Figure 2A shows the direction tuning curves of two simultaneously recorded neurons whose spatial receptive fields and preferred directions were very similar (ΔPD = 20°). To compute noise correlation on discrimination trials, we measured firing rates during the entire stimulus period (spike count divided by reaction time). We then transformed firing rates into Z scores, normalized the z scores for slow drifts in excitation, separated 0% coherence trials into same-pool and different-pool conditions and computed correlation coefficients on the normalized z scores for each context (see Experimental Procedures for details of these calculations). Normalizing for long-term drifts in firing rates removed the effect of any factor that changed slowly over the course of the experiment (e.g., arousal, motivation, intrinsic neural excitability), and for some pairs, changed the value of noise correlation we computed. This normalization did not, however, change the difference in noise correlation between our two contexts (data not shown).

Figure 2B is a scatter plot of Z scores measured in the same-pool condition for the pair of neurons in Figure 2A, and Figure 2C depicts the corresponding scatter plot for the different-pool condition. For this pair of neurons, the correlation coefficient was 0.445 in the same-pool context (one of the higher correlation

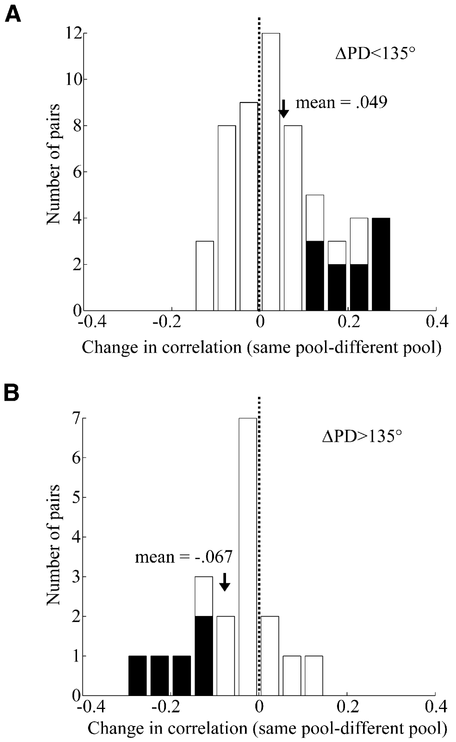

Figure 3. Frequency Histogram of Context-Dependent Differences in Noise Correlation

(A) Frequency histogram of context-dependent differences in correlation for pairs of neurons with ΔPD < 135°. The x axis plots correlation in the same-pool condition minus correlation in the different-pool condition. The black arrow indicates the population mean, and shaded bars indicate individual experiments for which this metric was significantly different from 0 ($p < 0.05$, bootstrap test described in Experimental Procedures).

(B) Same conventions, for pairs with ΔPD > 135°.

coefficients we observed), but only 0.167 in the different-pool context. The difference in correlation between the two contexts (0.278) was significantly different from 0 (bootstrap test, $p < 0.01$; see Experimental Procedures).

The effect of context on noise correlation illustrated in Figures 2B and 2C was generally true across our dataset of MT pairs when ΔPD was less than 135° (see below for explanation of this choice of criterion). Figure 3A shows the change in correlation measured for each of the 56 pairs in this subset of our data. The frequency histogram is shifted significantly to the right of zero, indicating that noise correlation was larger in the same-pool condition across this subset of MT pairs (t test, $p < 0.0005$). The effect was significant for each animal individually ($p < 0.001$ for monkey T, $p < 0.05$ for monkey D). Surprisingly, the sign of this effect was reversed for MT pairs whose ΔPD was *greater* than 135°. Figure 3B shows the change in correlation measured for each of the 19 paired recordings in this subset of our data. This distribution is shifted significantly to the left, indicating that noise correlation was higher in the *different-pool condition* across this subset of pairs (t test, $p < 0.05$). This effect was significant for monkey T individually (t test, $p < 0.05$). The same trend was present in Monkey D (mean change in correlation = -0.06), but the dataset was too small to reach statistical significance ($n = 6$).

These data are plotted in more detail in Figure 4A, showing more clearly how noise correlation varies with ΔPD. The magenta curve depicts the average noise correlation measured in the same-pool condition, with ΔPD binned in 45° increments. Noise correlation falls gradually as ΔPD increases. The green curve illustrates the equivalent data for the different-pool condition. Consistent with the frequency histograms in Figure 3, noise correlation is lower in the different-pool condition for all values of ΔPD except those greater than 135°, where the surprising reversal occurs. As indicated by the asterisks, the difference in noise correlation between the two task conditions is statistically significant for each bin. Note also that all average values of noise correlation are positive irrespective of the behavioral context or ΔPD, suggesting that some amount of common noise is present in the entire population of MT neurons that we sampled.

Noise Correlation during Passive Fixation

Recording pairs of MT neurons on a single electrode, Zohary and colleagues showed previously that noise correlation exists between pairs of MT neurons even when the monkey is fixating a small target on an otherwise blank screen (Zohary et al., 1994). This “spontaneous” noise correlation varied systematically with ΔPD, as did the noise correlation of visually evoked activity in their study. Because noise correlation did not depend upon task performance, or even upon the presence of a visual stimulus, Zohary and colleagues surmised that the observed correlations arose from hardwired common inputs, probably from antecedent visual areas such as primary visual cortex.

We replicated the key observations of Zohary and colleagues by measuring noise correlation during the fixation interval of our own experiments when no visual stimulus was present within the joint receptive field of the two MT neurons (see Figure 1A). The black data points in Figure 4A show the result. Our data confirm both key findings of Zohary and colleagues: (1) noise correlation decreases with increasing ΔPD, and (2) noise correlation is indistinguishable in the fixation and same-pool attention conditions (magenta line; paired t tests, $p > 0.05$ for each ΔPD bin, and $p = 0.34$ for the entire population). The new observation in our data is that noise correlation is altered in the different-pool condition, being significantly lower than the fixation period for ΔPD < 90° (paired t tests, $p < 0.05$ for each bin). For larger ΔPD, noise correlation in the different-pool condition was not statistically different from the fixation period (paired t tests, $p > 0.05$ for each bin, and $p = 0.26$ for the two bins together), although the upward trend for ΔPD > 135° approached significance.

Noise Correlation during the Target Period

We inquired whether the context-dependent correlation effects are also present during the target period, or whether the context-dependent effects are present only when a visual stimulus appears within the receptive fields of the two neurons. Recall that during the target period the monkeys are fully informed about the axis of motion to be discriminated, but the random dot stimulus has not yet appeared (see Figure 1A and Experimental Procedures). We calculated noise correlation during the target period in our task using the same methods we applied

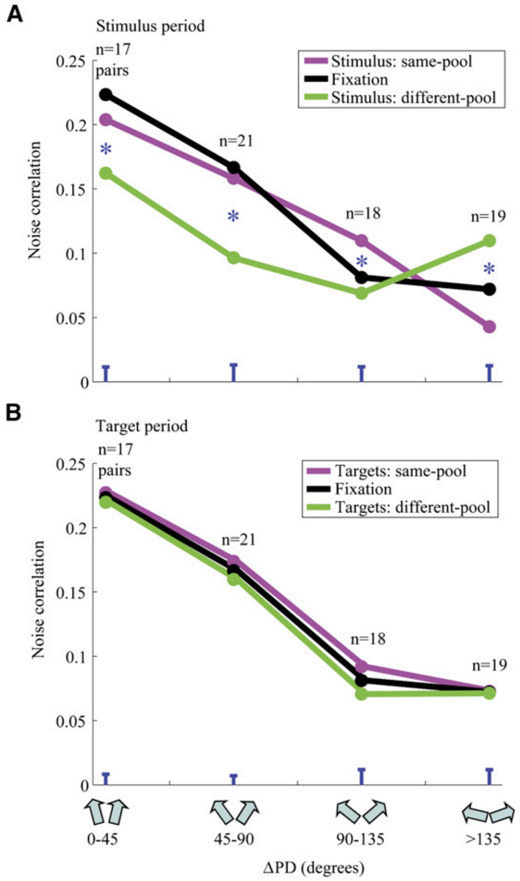

Figure 4. Noise Correlation as a Function of ΔPD

(A) Mean noise correlation during the stimulus period in each of four ΔPD bins for the same-pool (magenta) and different-pool (green) conditions. The black line represents noise correlation during the initial fixation period (while the monkey fixated a blank screen). The asterisks indicate that mean noise correlation was significantly different in the same and different-pool conditions for each bin. Because noise correlation even during the fixation period varied substantially from pair to pair even within a ΔPD bin (for example, mean fixation correlation for the $\Delta PD < 45^\circ$ bin was 0.223, and standard deviation was 0.180), all of our statistics were based on the pairwise difference in correlation between the same- and different-pool contexts for each pair. The blue error bars at the bottom of (A) and (B) indicate standard errors on these differences for each bin.

(B) Conventions are the same as in (A), but the magenta and green lines are correlation during the target period. The black line is the same as in (A). There were no bins for which the difference in correlation between the same and different-pool conditions was statistically significant.

during the visual stimulus period. Figure 4B displays the results in the same format employed for the visual stimulus period data in Figure 4A. For ease of comparison, data from the fixation period (Figure 4A, black line) are replotted in Figure 4B as well.

Noise correlation during the target period was not different from fixation during either the same-pool condition (paired t test on the entire population, $p = 0.18$) or the different-pool condition (paired t test, $p = 0.21$), and the same- and different-pool results were not significantly different from each other (paired t test, $p = 0.19$). The lack of an effect during the target period might indicate that context-dependent changes in functional circuitry occur only while the monkey is actively engaged in perceptual decision-making or that the context-dependent signal acts in a way that is dependent on the firing rates of MT neurons (mean firing rate was 9.7 spikes/s during the target period compared to 28.5 spikes/s and 8.2 spikes/s for the stimulus and fixation periods, respectively).

Relationship between Noise Correlation and Behavioral Choice

As has been reported previously (Britten et al., 1996; Dodd et al., 2001; Cook and Maunsell, 2002; Barberini et al., 2005; Krug et al., 2004; Liu and Newsome, 2005), we observed a small but significant correlation between trial-to-trial fluctuations in the neurons' responses and the monkey's choices (“choice probability”; see Britten et al., 1996, for methods and see also M.R.C. and W.T.N., 2004, Soc. Neurosci., abstract). We therefore analyzed our data to identify any possible relationship between the monkeys' choices on individual trials and our noise correlation measurements. We first calculated noise correlation separately on trials in which the monkey chose each possible direction of motion. Within a given context, the resulting distributions of noise correlation were indistinguishable between choice conditions (t test, $p = 0.41$ for the same-pool condition and $p = 0.72$ for the different-pool condition). We then calculated the difference between the responses of the two neurons on individual trials and searched for any correlation between this difference in firing rates and behavioral choice on a trial-to-trial basis. Again, we could find no correlation ($p = 0.56$, bootstrap test).

Lack of Context Dependence of Other Measures of Neural Activity

Firing Rate and Variance

The results in Figures 3 and 4 show that context-dependent correlation changes occur during the stimulus period and not during the target period (when firing rates are very low). The fact that changes are absent during a period of low firing rates is a signature of processes that change the gain of sensory responses in a multiplicative way. Indeed, the most well-studied top-down influences on MT firing rates, spatial and feature-based attention (Treue and Maunsell, 1996, 1999; Seidemann and Newsome, 1999; Treue and Martinez-Trujillo, 1999; Cook and Maunsell, 2002, 2004; Martinez-Trujillo and Treue, 2004; Maunsell and Treue, 2006), are thought to change the gain of MT responses. We therefore suspected that our correlation results may be caused by a process that changes gain as well.

Multiplicative gain changes have traditionally been associated with changes in firing rate and variance rather than noise correlation, so we looked for evidence of such changes in our dataset. Figure 5 shows the percent difference in firing rate (Figure 5A) and variance (Figure 5B) for each neuron between the same-pool condition and the different-pool condition during the stimulus period for 0% coherence trials. Positive percent change indicates a higher rate or variance in the same-pool condition. Although a higher percentage of neurons showed significant changes in rate (18.7%) or variance (11.3%) than would be expected by chance ($p < 0.05$, t test), these significant changes included both increases and decreases, and the mean of neither the rate nor variance distribution was significantly different

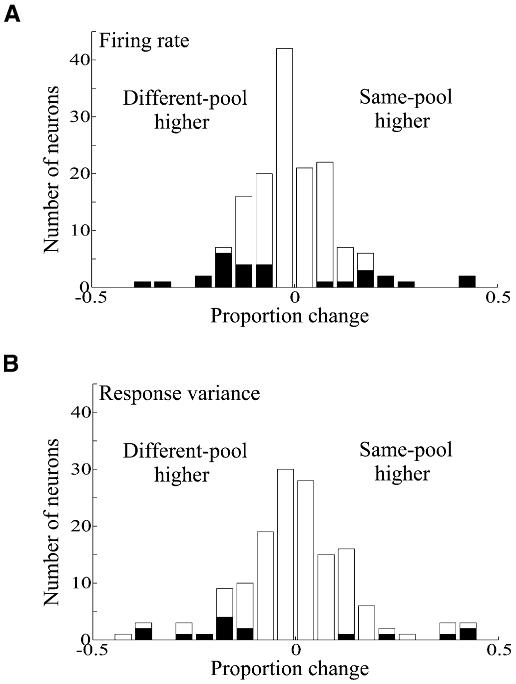

Figure 5. Absence of Context-Dependent Changes in Firing Rate and Variance

(A) Frequency histogram of context-dependent changes in firing rate. The x axis represents the proportion change in firing rate [(same pool-different pool)/different pool] on 0% coherence trials for each MT neuron. Shaded bars indicate cells that had individually significant context-dependent changes in firing rate ($p < 0.05$, t test).

(B) Conventions as in (A), but for variance rather than mean firing rate.

from zero (p = 0.67 for rate, p = 0.32 for variance). Therefore, context exerted no consistent effect on either rate or variance. Furthermore, neither rate change nor variance change was significantly correlated with a neuron's arithmetic or geometric mean firing rate, arithmetic or geometric mean variance, noise correlation, change in noise correlation, direction selectivity index, tuning curve width, neurometric threshold, choice probability, or the difference between its preferred direction and the axis of motion being discriminated (data not shown). Therefore, whatever mechanism accounts for the context-dependent change in noise correlation that we see during the stimulus period does not consistently affect firing rate or variance during 0% coherence trials.

Precise Spike Timing Synchrony

The results presented thus far show that spike rate noise correlation is dependent on the axis of motion the monkey is discriminating. This is consistent with correlation changes on either or both of two possible timescales. One possibility is that synchrony on the millisecond timescale, as has been postulated to underlie other cognitive processes, is modulated by context (e.g., Kreiter and Singer, 1996; Reynolds and Desimone, 1999; Steinmetz et al., 2000; Fries et al., 2001; Taylor et al., 2005; Bichot et al., 2005; Bichot and Desimone, 2006, but see Palanca and DeAngelis, 2005). The other plausible possibility is that the context-dependent changes in spike count correlation are a result of changes in correlation on the timescale of tens of milliseconds as has been shown to exist in MT (Bair et al., 2001) as well as other visual areas (Gawne and Richmond, 1993; Gawne et al., 1996; Reich et al., 2001; Kohn and Smith, 2005). Note that our results cannot be explained by correlation on the timescale of several seconds or longer because our stimulus presentations were only a few hundred milliseconds long, we corrected for long-term drifts in firing rate, and the two contexts were randomly interleaved (see Experimental Procedures for details of this normalization).

To investigate whether our results can be explained by context-dependent changes in precise spike timing synchrony, we first compared the measured cross correlogram (CCG) for each pair to a shuffled CCG for each pair. Since each trial had a different stimulus duration, we only analyzed the first 250 ms of trials that were at least that long (99.55% of trials for Monkey T and 99.16% of trials for Monkey D). To compute the shuffled CCGs, we randomly assigned 0% coherence trials to the two neurons, recomputed the new cross-correlogram and then calculated the mean and 95% confidence intervals of these shuffled CCGs (10,000 reshuffles). We found that only 13/75 pairs (17.3%) showed significant synchrony from -10 to +10 ms in the CCG in at least one of the contexts (measured CCG lay outside the 95% confidence interval for the shuffled CCG), and only 9/75 pairs (12%) showed significant synchrony in both contexts. Therefore, most of the pairs of neurons in our dataset do not show evidence of precise spike timing synchrony that survives the shuffle analysis.

To test whether any small changes in synchrony are context dependent, we subtracted the integral of the measured CCG from -10 to 10 ms in the different-pool condition from that in the same-pool condition. We found that differences in synchrony were not significantly correlated with differences in firing rate correlation (p = 0.27), nor were they correlated with ΔPD (p = 0.76). Taken together, these results indicate that precise spike timing synchrony is not substantially present in our dataset and cannot account for the context-dependent modulation of noise correlation that we observed.

Eye Movements and Position

Interpretation of our results depends on the fact that the only difference between our two contexts is the axis of motion that the monkey thinks he is discriminating. We enforced fixation throughout the trial (the fixation window radius was typically 1° for Monkey T and 1.5° for Monkey D), but small fixational eye movements or differences in eye position between the two conditions could potentially alter our results (Bair and O'Keefe, 1998). Monkey T made a fixational saccade of >0.3° during the stimulus period in 9.8% of 0% coherence trials, and Monkey D made a fixational saccade in 12.1% of 0% coherence trials. We did not include these trials in the above analyses (and including them did not qualitatively affect our results).

We also measured the monkeys' eye position within the fixation window during the stimulus period. We found that on some days, there was a slight but significant difference in mean eye position between the two axes of motion. Eye position was also sometimes correlated with the animal's choice (upcoming eye movement) on a given trial. We believe, however, that these small changes in eye position do not influence our results.

Eye position is likely to be correlated with the axis of motion and target locations rather than with task condition. The designation of an axis as the same-pool or different-pool condition depended solely on the preferred directions of the two neurons on our electrodes. Therefore, for example, up-down discrimination could be the same-pool condition on one day and the different-pool condition on another day, so any change in eye position due to the physical axis should affect both contexts equally when averaged over many days. Indeed, there was no difference in mean eye position between the same-pool trials and different-pool trials when combined across days, as we did for all of our analyses. Furthermore, noise correlation was not correlated with the eye movement the monkey eventually made (behavioral choice; data not shown). We therefore conclude that fixational saccades, mean eye position, and eye movement planning cannot account for the systematic differences in correlation that we saw between the two contexts.

Possible Mechanism of Context-Dependent Effects on Noise Correlation

Our physiological results suggest that MT receives a top-down or recurrent input that is dependent on the axis of motion the monkey discriminated. In our direction-discrimination task, the appearance of the saccade targets cues the animal to discriminate along a particular axis of motion—a process that seems qualitatively similar to feature-based attention. We ran simulations to test whether a process like feature-based attention is a feasible explanation for our noise correlation results.

Feature-based attention is thought to affect the gain of visual responses in several brain areas including MT (for review, see Maunsell and Treue, 2006). In a particularly elegant study, Martinez-Trujillo and Treue (2004) recorded from MT neurons while monkeys attended a random dot motion stimulus outside the neuron's receptive field. They found that the gain of the neuron's response to a second, unattended stimulus in the neuron's receptive field was modulated by the difference between the preferred direction of the neuron under study and the direction of motion the animal was attending. Martinez-Trujillo and Treue developed a "feature-gain-similarity model" to explain these results; the model postulates that feature-based attention improves detection of the attended feature by increasing the selectivity of the entire population of neurons that is selective for the attended direction of motion.

In our task, unlike the task used by Martinez-Trujillo and Treue (2004), the monkey needs to attend to two opposite directions of motion. For example, in the context of an up-down discrimination task, the best strategy would be to attend simultaneously to both upward and downward motion and ignore rightward and leftward motion. We have no way of knowing, however, whether our monkeys can attend effectively to two directions simultaneously. Another strategy would be to alternate attention between the two relevant directions of motion (e.g., attend up on some trials or moments and down on others while ignoring motion to the right and left). Interestingly, the simulations described below show that a mixture of these two strategies qualitatively reproduces the main features of our physiological data.

Although our task does not provide a behavioral measure of attentional modulation with which to constrain a quantitative model, we can predict qualitative effects of both strategies on noise correlation if we make two conservative assumptions about the way attention affects sensory responses. The first assumption is that attention acts by changing the gain of MT responses. Following Martinez-Trujillo and Treue (2004), we assume that gain depends on the difference between a neuron's preferred direction (or axis of motion) and the attended feature (direction in the first strategy, motion axis in the second), as in the feature-gain-similarity model. According to this assumption, the firing rate of an MT neuron could be written:

$$r_i = s_i(1 + g(\phi)) = s_i + g(\phi)s_i, \tag{1}$$

where r_i is the response of the ith MT neuron to a given stimulus when the animal is in a particular attentional state, s_i is the response to the same stimulus when the animal is not attending to it (i.e., the sensory, bottom-up response; see Supplemental Data for details on simulating sensory responses), and g is the gain term that depends on ϕ, which is equal to the angle between the neuron's preferred direction and the attended direction or axis (Martinez-Trujillo and Treue, 2004; Maunsell and Treue, 2006). Various estimates for the value of the gain term (for MT neurons) have been made by different authors (Cook and Maunsell, 2002, 2004; Treue and Maunsell, 1996, 1999; Seidemann and Newsome, 1999). For simplicity, we adopt the gain function suggested by the results in Martinez-Trujillo and Treue (2004), in which $g(\phi)$ varies linearly from 0.1 (a 10% increase) when the monkey attends to the neuron's preferred direction ($\phi = 0°$) to -0.1 when the monkey attends to the neuron's null direction ($\phi = 180°$). Qualitatively, the pattern of results in the simulations below are not sensitive to the particular gain function chosen; similar results are obtained for any function that decreases monotonically as ϕ increases. The $g(\phi)s_i$ term in Equation 1 could be thought of as a top-down or feedback input to MT.

The second assumption is that attention is not constant from trial to trial. That is, we assume that there is trial-to-trial variability in the gain of an MT neuron's response, so the gain term, $g(\phi)$, in Equation 1 is noisy. Therefore, the top-down input to MT can be written:

$$[g(\phi) + \varepsilon]s_i,$$

where ε is a noise term. In our simulations, we assumed that ε is zero-mean, Gaussian noise whose variance is proportional to the gain term, $g(\phi)$. Thus our full model for the response of an MT neuron is

$$r_i = [1 + g(\phi) + \varepsilon]s_i. \tag{2}$$

We ran simulations to assess the pattern of noise correlation obtained under the two attentional strategies discussed above. Consider a set of trials in which the monkey is asked to discriminate up from down motion. In the "alternating attention" strategy, the monkey attends to a single direction of motion, alternating between up and down on different trials. This strategy would result in noise correlation being higher in the same-pool condition than in the different-pool condition for all pairs of neurons (Figure 6A). This effect can be appreciated by considering the pair of neurons in the schematics in the left side of Figure 6A in which one neuron prefers motion up and slightly left, while the

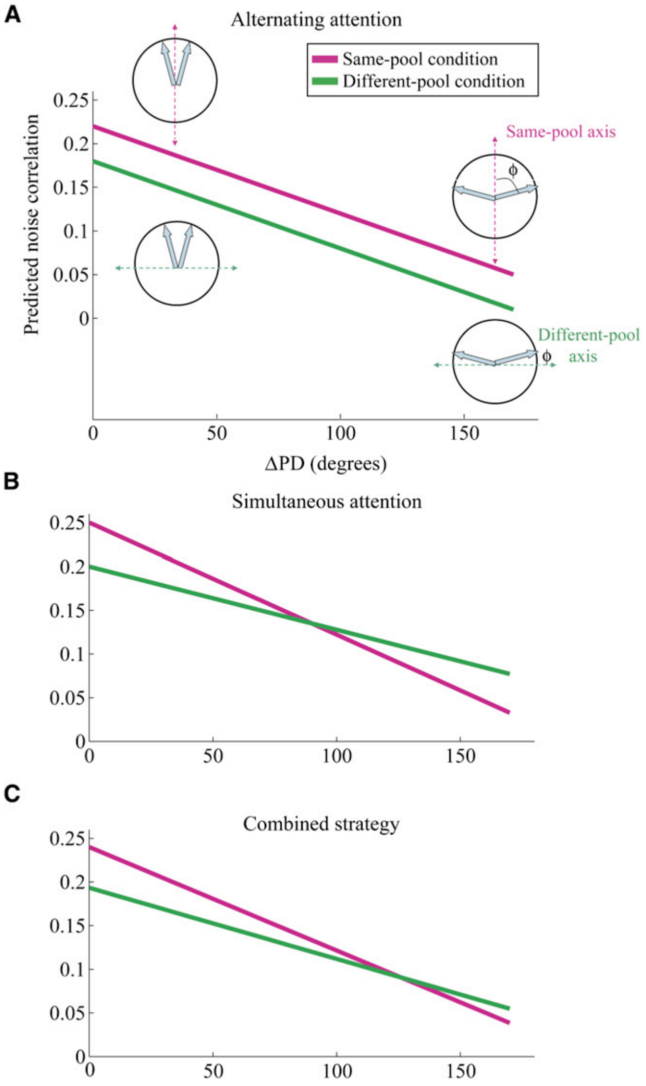

Figure 6. Noise Correlation Predictions from a Feature-Attention-like Mechanism

Conventions are the same as Figure 4.

(A) Prediction noise correlation if the monkey employed the “alternating attention” strategy. The four schematics in the corners of the graph show the relationship between the preferred directions of the two hypothetical neurons under study (blue arrows) and the axis of motion in the same-pool condition (magenta dashed line) and the different-pool condition (green dashed line).

(B) Conventions as in (A), for the “simultaneous attention” strategy.

(C) Conventions as in (A), for a combined strategy (see text).

other prefers motion up and slightly right. These neurons will be in the same pool on an up-down trial (top-left schematic in Figure 6A). When the monkey attends up, attention will cause the firing rates of both neurons to increase, and when he attends down, the firing rates of both neurons will decrease. Therefore, the firing rates of the two neurons fluctuate up and down together resulting in a positive noise correlation. In the different-pool condition (right-left discrimination, bottom-left schematic), if the monkey attends left, the firing rate of one neuron will increase while the other decreases, and the effect will reverse when the monkey attends right. This will introduce a small amount of anti-correlation for these two neurons, resulting in a decrease from the positive baseline noise correlation. The same basic pattern of results will hold for pairs of neurons with large ΔPD (top-right and bottom-right schematics in Figure 6A).

In contrast, the “simultaneous attention” strategy, in which the monkey attends to an entire axis of motion, would result in a very different pattern of noise correlation changes, as illustrated in Figure 6B. These simulation results are particularly interesting because they exhibit the peculiar reversal of the noise correlation effects at large ΔPD that we saw in the physiological data (Figure 4A). To appreciate this result intuitively, consider again the recording geometries outlined in Figure 6A. When ΔPD is small in the same pool condition (top-left schematic in Figure 6A), attentional modulation of the two neurons will be strong on average because the preferred directions of the two neurons are both close to the attended axis (ϕ is close to 0), and positive noise correlation will be generated because the amplitude of the attentional modulation varies from trial to trial (Equation 2, magenta line in Figure 6B). When the same two neurons are in different pools (bottom-left schematic in Figure 6A, left side of the green line in Figure 6B), however, ϕ is large, so attentional modulation is small, and noise correlation is unaffected. For small ΔPD, therefore, the pattern of expected noise correlation is similar for both attentional strategies (Figures 6A and 6B); noise correlation should be higher in the same-pool condition.

For large ΔPD, however, the sign of the effect reverses. Noise correlation is strong in the different-pool condition (bottom-right schematic in Figure 6A, right side of the green line in Figure 6B), because both preferred directions lie close to the attended axis of motion and are therefore strongly modulated by attention. Conversely, attention does not strongly affect noise correlation in the same-pool condition (top-right schematic in Figure 6A, right side of the magenta line in Figure 6B) because the preferred directions differ substantially from the attended axis. This strategy predicts that for ΔPD = 90°, noise correlation should be equal in the two conditions.

Our physiological data are in fact most consistent with a combination of the two behavioral strategies (Figure 6C). For most pairs of neurons, noise correlation was higher in the same-pool condition than in the different-pool condition, consistent with the “alternating attention” hypothesis. For neurons with large ΔPD, however, noise correlation was on average higher in the different-pool condition, which is consistent with the “simultaneous attention” strategy. Figure 6C plots predicted noise correlation if the monkey applied “simultaneous attention” strategy with twice the strength of the “alternating attention” strategy (the weight of the top-down input from the simultaneous attention strategy is twice that of the alternating attention strategy). Our experimental design does not allow us to quantitatively constrain these models, but the results in Figure 6C show that a combination of the two attentional strategies is a plausible explanation for our noise correlation results.

DISCUSSION

The goal of this study was to detect context-dependent changes in functional circuitry by measuring changes in the noise correlation between pairs of MT neurons. Our primary finding was that, during 0% coherence trials, noise correlation depended not only on the difference in the preferred directions of the two neurons (Zohary et al., 1994; Bair et al., 2001), but on whether the responses of the two neurons contributed to the same or opposite perceptual decisions. For pairs of neurons with relatively similar preferred directions, noise correlation was on average higher in the same-pool condition, but for pairs of neurons with very different preferred directions, noise correlation was higher in the different-pool condition. Furthermore, this context-dependent difference was only present during the stimulus period, when the monkey was actively making a perceptual decision and the stimulus was in the neurons' receptive fields. In the target period, when the monkey knew the axis of motion for the upcoming trial but had not yet seen the stimulus, noise correlation was not significantly different than during the fixation period.

If the observed changes in noise correlation are truly related to context, then they must be due to changes in functional inputs of central origin. That is, the strength of top-down or recurrent connections to MT must change in a task-dependent way. Here, we review evidence that the changes we see cannot be solely due to changes in non-context-dependent functional inputs and suggest possible sources of context-dependent top-down or recurrent signals.

Possible Artifacts

The primary source of concern regarding the soundness of our conclusions is the possibility that some aspect of the visual display (e.g., exact locations of the saccade targets relative to the fixation point or the receptive fields) or the monkey's behavior (e.g., fixational eye movements or eye position) differed systematically between the two behavioral contexts, introducing an external cause for the observed changes in noise correlation. It is essential to realize, however, that differences in the visual display or the monkey's behavior did not vary systematically with the "same-pool" or "different-pool" designation, which is the critical designation in all of our analyses. Consider, for example, the visual displays illustrated in Figure 1A. By design, these displays vary markedly between the up-down and right-left discrimination conditions, and in some experiments we in fact observed small but significant differences in mean fixational eye position between the two conditions (see Results). Importantly, however, the same-pool and different-pool designation was based entirely on the preferred directions of the two neurons under study, not on the physical layout of the visual display. Thus, the up-down axis would serve as the same-pool axis for some experiments and as the different-pool condition for others. In general, any aspect of the monkey's behavior (and consequent receptive field stimulation) that varies with the physical layout of the visual display will not be systematically correlated with the same-pool and different-pool designations. While differences may occur in individual experiments, such effects should average out between same-pool and different-pool conditions across the accumulated dataset (we in fact verified this empirically for average eye position and frequency of fixational saccades).

A similar argument applies to artifacts that might arise from subtle variations in neural activity caused by the random dot stimuli themselves or by the reaction-time task design. We eliminated large differences in visually-driven activity between the same-pool and different-pool conditions by restricting our analysis to 0% coherence trials which are identical, on average, across the conditions. The stimuli differed subtly across trials, however, because we used a different random-number seed on each trial; this stimulus variation could lead to small amounts of covariation in the activity of MT neurons. Similarly, spike rates may covary subtly from trial-to-trial because of the differences in reaction-time – shorter reaction times will overemphasize the initial onset transient of the response relative to longer reaction times. But again, our analysis is based on differences in noise correlation between same-pool and different-pool conditions. Thus it only matters that any stimulus variations that could result in response covariation are the same on average between the same-pool and different-pool conditions. While stimulus variation might subtly affect the absolute level of noise correlation (but see Zohary et al., 1994), it should have no effect on the differences in noise correlation between the two conditions.

Other possible sources of artifact can be ruled out as well: (1) We always attempted to place the saccade targets outside the neurons' classical receptive fields. A portion of the neurons in our dataset showed significant firing rate changes associated with target onset (31/150 = 20.7%) but omitting these cells from our analyses did not qualitatively change our results (data not shown). Furthermore, we did not observe any changes in noise correlation at the time of target onset (Figure 4B). (2) All coherences and both behavioral contexts were randomly interleaved during each experiment. Thus any slow changes during the course of a recording session (e.g., average neural excitability, the monkey's arousal or motivation, or the quality of spike isolation) should affect both contexts equally. We also normalized neural firing rates using a sliding mean to prevent slow changes in firing rates from affecting our correlation results (see Experimental Procedures). (3) All of our analyses include only trials in which there were no detectable fixational saccades during the stimulus period, and including such trials did not qualitatively alter our results (data not shown).

Another possible explanation for some of our results is that our observed changes in noise correlation are simply an artifact of choice probability, the correlation between the trial-to-trial fluctuations in neural responses and the monkey's behavioral judgment (see Britten et al., 1996). This argument predicts that noise correlation should be higher in the same-pool condition than the different-pool condition because if two neurons' responses are correlated with the same perceptual judgment (same-pool condition), then they should be correlated with each other. Similarly, if the fluctuations in the responses of two neurons are correlated with opposite decisions (different-pool condition), they should be anticorrelated with each other. We ran simulations to assess the possible contribution of choice probability to our measured noise correlation, and we found that choice probability effects are too weak to account quantitatively for the context-dependent changes in noise correlation we observed (see Supplemental Data).

Top-Down or Recurrent Processes that Could Underlie Correlation Changes

We therefore conclude that the changes in correlation observed during the stimulus period are due to changes in top-down or recurrent functional inputs to MT whose strength is context-dependent. In our direction-discrimination task, the appearance of the saccade targets cues the animal to discriminate along a particular axis of motion—a process that seems qualitatively similar to feature-based attention. Feature-based attention is thought to affect the gain of visual responses in several brain areas including MT (for review, see Maunsell and Treue, 2006), and we sought to understand our noise correlation data by performing simulations based on the feature-gain-similarity model introduced by Martinez-Trujillo and Treue (2004).

Our simulations (Figure 6) suggest that a combination of two attentional strategies can qualitatively account for our data. In one strategy, the monkey attends simultaneously both directions of the relevant axis of motion; in the other the monkey alternates attention between the two opposite directions. Our data do not allow us to constrain such a model quantitatively because we have no way to determine empirically whether and how the monkey's attentional strategy actually shifts between these two modes. Nevertheless, the simulations show that a process like feature-based attention could provide top-down inputs that resulted in the noise correlation changes we observed.

Further experiments will be needed to determine whether attention indeed operates by adding a common input to neurons representing the attended feature (thereby changing noise correlation). Feedback from pre-oculomotor areas such as the frontal eye fields and the superior colliculus is thought to underlie the top-down gain changes in sensory responses that occur in cognitive processes such as spatial attention (Moore and Fallah, 2001; Moore and Armstrong, 2003; Moore et al., 2003; Cavanaugh and Wurtz, 2004; Muller et al., 2005). This sort of feedback could provide the dynamic functional input to MT that caused the changes in noise correlation we observed.

Concluding Remarks

By measuring changes in noise correlation in pairs of MT neurons, we have shown that functional circuitry changes in accordance with changes in the spatial structure of a direction discrimination task. This finding is important for several reasons. First, this study demonstrates that changes in noise correlation can be used to detect task-dependent changes in functional circuitry, even when firing rates are not task-dependent (see also Vaadia et al., 1995). Second, this result shows that in our system, the context-dependent changes in functional circuitry occur within or before MT, which is a sensory area positioned at a relatively early stage of the sensorimotor pathway. These changes could well have occurred at the level of the neurons that read out MT responses, in which case we would have seen no changes at the level of MT. Finally, the pattern of correlation changes provides clues concerning the nature of the task-dependent circuitry changes.

EXPERIMENTAL PROCEDURES

We recorded from 75 pairs of single MT neurons in four hemispheres of two adult male rhesus monkeys (*Macaca mulatta*, weight 13–15 kg; 50 pairs of neurons for Monkey T and 25 pairs for Monkey D). Prior to the recordings, we surgically implanted each animal with a scleral search coil for measuring eye movements (Judge et al., 1980), a head holding device (Evarts, 1968), and a recording cylinder (Crist Instruments, Damascus, MD) that provided access to MT. The monkeys performed a visual discrimination task for liquid rewards while seated in a primate chair, facing a CRT monitor. All surgical and behavioral procedures conformed to guidelines established by the National Institutes of Health and approved by the Institutional Animal Care and Use Committee of Stanford University.

Behavioral Task and Visual Stimuli

We trained both monkeys to perform a reaction-time version of a 2AFC motion direction discrimination task in which monkeys discriminated opposed directions of motions in a stochastic random dot display (Newsome and Pare, 1988; Newsome et al., 1989; Roitman and Shadlen, 2002; see Figure 1A). The monkeys fixated a central spot of light for 200 ms ("fixation period"), and then two saccade targets appeared, indicating to the monkey which of two orthogonal axes of motion he was to discriminate ("target period"). The duration of the target period was selected from a truncated exponential distribution (min 150 ms, mean 700 ms, max 1800 ms) in order to discourage anticipation of the stimulus onset (Roitman and Shadlen, 2002). The motion stimulus then appeared ("stimulus period") within the joint receptive field of the MT neurons under study. Following onset of the visual stimulus, the monkey was free to indicate his direction choice at any time by making a saccadic eye movement to one of the two targets flanking the stimulus. When the monkey's eye left the fixation point, the fixation point and motion stimulus disappeared leaving only the two saccade targets present on the screen. Two types of trials were considered to be "non-decisions" and were excluded from further analysis: (1) trials in which the monkey did not immediately make a saccade to one of the targets when his eyes left the fixation point, or (2) trials in which the monkey viewed the dots for more than 5 s without making an eye movement.

We used stochastic random-dot stimuli that were similar to those used in many previous studies (e.g., Britten et al., 1992; Roitman and Shadlen, 2002). We varied the strength of motion, and therefore the difficulty of the task, by changing the probability that on a given frame, a given dot was replotted in apparent motion in one of two opposite directions ("percent coherence"). For trials in which all of the dots moved randomly (0% coherence), we rewarded the monkey randomly with a probability of 0.5. For all other trials, we rewarded the monkey for correctly reporting the direction of coherent motion.

To prevent the monkey from using low-level visual cues to solve the task (e.g., when a dot appears in the upper right-hand corner of the screen, the correct answer is left), we used a new seed for our random number generator on each trial. Thus, the specific pattern of dot placement was different on each trial. Trial-to-trial differences in the dot placements can generate small, random fluctuations in motion energy presented to the receptive field, which could in principle cause trial-to-trial correlations in firing rate like those reported in this paper. Controls performed in a small sample of MT cells suggest, however, that such stimulus-driven correlations account for only a minor component (if any) of the trial-to-trial correlations reported in our experiments (Zohary et al., 1994). Most importantly, the primary results reported this paper result from a comparison of correlated firing in two behavioral conditions. Any stimulus-driven correlation due to the variable coherence dot displays would not differ between behavioral conditions.

Recording Methods

We recorded extracellular action potentials from pairs of well-isolated, direction selective MT neurons on separate microelectrodes using standard techniques (e.g., Britten et al., 1992). At the beginning of each recording session, we inserted a stainless-steel guide tube 1–3 mm past the dura, and we clamped two tungsten microelectrodes (Fred Haer, Bowdoinham, ME; 0.8–3 Mohm) together such that their tips were separated slightly in depth (approximately 200–800 μm). We advanced both microelectrodes through the guide tube into the brain using a hydraulic microdrive (Narishige, Tokyo, Japan). We identified MT by the pattern of gray and white matter transitions during descent, the topographic organization of MT, and the well-known electrophysiological properties of MT neurons. We isolated neurons through a spike waveform template matching algoritihm (EXPO, Peter Lennie) and we recorded the full waveform as well as the time of occurrence of each action potential.

Experimental Protocol

The experiment began when we isolated an MT neuron on each of two microelectrodes. We first qualitatively assessed the receptive field location and size, and the preferred speed and direction of each neuron. For most neurons, we then confirmed direction tuning by measuring the neuron's response to 500 ms presentations of fully coherent motion in 8 directions while the monkey fixated a central spot of light. We then fit the resulting tuning curves with a circular Gaussian to determine the preferred direction (direction at which the best-fit Gaussian was maximal) for each neuron. We only recorded from neurons whose distributions of responses to fully-coherent motion in the preferred and anti-preferred directions were non-overlapping.

We next established the axes of motion that would serve as the two behavioral contexts (Figure 1C). The "same-pool" condition was discrimination about the axis of motion that bisected the angle between the two neurons' preferred directions (top panel, dotted magenta line). The different-pool condition was the axis orthogonal to the same-pool axis (bottom panel, dotted green line). We selected pairs of neurons whose receptive fields overlapped by at least 75% (measured qualitatively), and we placed the stimulus in roughly the overlapping portion of the two neurons' receptive fields, and we chose the motion speed that best elicited a robust response from both cells.

The context (axis of motion), the direction of motion, and the motion coherence were randomly interleaved on each trial. We only included datasets for analysis in which each trial type was repeated a minimum of 25 times. Because 0% coherence trials were particularly important for analysis, we presented more 0% coherence stimuli than other coherences, so that in the datasets we included for analysis, 0% coherence trials were repeated at least 100 times for each behavioral context.

Data Analysis

In a reaction-time task like the one employed in this study, trial duration varies as a function of the timing of the animal's operant response, which raises issues concerning the appropriate time window for data analysis. For example, the visual transient, which is a period of characteristically high firing rate near the beginning of the stimulus presentation, will contribute more to the firing rate for short trials than for long trials. Also, the "motor preparation time"—the interval after the decision has been made but before the saccade is executed—can comprise a non-trivial fraction of the entire reaction-time (as much as 300 ms, see Mazurek et al., 2003).

We therefore experimented with excluding portions of the initial transient response and portions of the motor preparation time from our analyses, as well as using fixed durations locked to either stimulus onset or the saccade. Within reasonable limits, however, these manipulations did not significantly affect the calculated task-dependent changes in noise correlation, firing rate, or variance. We therefore selected the simplest option, calculating the firing rate on each trial (spike count divided by reaction time) for the entire stimulus duration prior to saccade onset. For most calculations, we only analyzed 0% coherence trials; the mean reaction time for these trials was 585 ms for Monkey T and 674 ms for Monkey D.

We normalized spike rates on each trial for both mean firing rate and slow drifts in neural excitation by computing a z score for each neuron's firing rate on each trial using a sliding window of twenty 0% coherence trials before and after the current trial (regardless of context). Therefore, the z score for the *i*th neuron on trial *k* was:

$$z_i(k) = \frac{r_i(k) - \mu_i}{\sigma_i},$$

where $r_i(k)$ is the firing rate on trial *k*, and σ_i and μ_i are the variance and mean of the *i*th neuron's firing rates on the previous and future twenty trials. We then computed the correlation coefficient of those z scores separately for the two contexts.

We tested for significantly different correlation coefficients in the two contexts in individual experiments using a bootstrap test in which we computed correlation coefficients for randomized context assignment and then compared the actual correlation difference to the distribution of correlation differences calculated for the randomly assigned data.

The data in Figure 5 came from measurements of firing rate and variance during the same time period in which correlation was calculated (stimulus onset to the time that the eyes left the fixation window). Firing rate and variance are presented as % change, which we defined as

$$\frac{x_{same-pool} - x_{different-pools}}{x_{different-pools}},$$

where *x* is the (nonnormalized) firing rate mean or variance, respectively.

We excluded from analysis trials in which the reaction time was greater than 3 s. Because small fixational saccades can generate correlated bursts of firing in MT neurons (Bair and O'Keefe, 1998), we also excluded trials in which the monkey made a small fixational saccade within the electronic fixation window. We defined a fixational saccade as displacement of at least 0.3° within a 50 ms time period. Monkey T made a fixational saccade during the stimulus period in 9.8% of 0% coherence trials, and Monkey D made a fixational saccade in 12.1% of 0% coherence trials.

SUPPLEMENTAL DATA

The Supplemental Data include an analysis of the relationship between noise correlation and choice probability and Supplemental Experimental Procedures for the model presented in Figure 6 and can be found with this article online at http://www.neuron.org/supplemental/S0896-6273(08)00675-2.

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