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Effects of Attention on the Reliability of Individual Neurons in Monkey Visual Cortex

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Summary

To determine the physiological mechanisms underlying the enhancement of performance by attention, we examined how attention affects the ability of isolated neurons to discriminate orientation by investigating the reliability of responses with and without attention. Recording from 262 neurons in cortical area V4 while two rhesus macaques did a delayed match-to-sample task with oriented stimuli, we found that attention did not produce detectable changes in the variability of neuronal responses but did improve the orientation discriminability of the neurons. We also found that attention did not change the relationship between burst rate and response rate. Our results are consistent with the idea that attention selects groups of neurons for a multiplicative enhancement in response strength.

Introduction

Attention can dramatically affect our perception of the world. Psychological experiments, as well as our intuition, suggest that attention improves neuronal processing (Rensink et al., 1997; Simons and Levin, 1997). Neurophysiological studies have demonstrated that attention can increase neural responses to a particular stimulus (Desimone and Duncan, 1995; Maunsell, 1995). This study concerns how attention affects the reliability of the responses produced by individual neurons and thereby leads to improvements in neuronal signaling.

The ability of a neuron to provide signals that distinguish stimuli depends on two factors: the difference in the response to two stimuli (signal) and the variability of those responses (noise). If attention systematically improved either of these factors, it could improve the performance of sensory neurons in a way that might contribute to or account for improvements in behavioral performance.

The effects of attention on the first factor, the signal, have been examined in several studies that have measured how attention affects the mean rate of firing elicited by particular stimuli (Bushnell et al., 1981; Mountcastle et al., 1981; Moran and Desimone, 1985; Haenny and Schiller, 1988; Haenny et al., 1988; Maunsell et al., 1991; Motter, 1994; Treue and Maunsell, 1996). Other studies in which neuronal tuning curves were constructed under different behavioral conditions have shown that attention increases responses to all stimuli proportionally and does not improve the selectivity of single neurons, as measured by the width of their tuning curve (Vogels and Orban, 1991; Motter, 1993; McAdams and Maunsell, 1999). Instead, all signals appear to be multiplicatively scaled by attention.

The effects of attention on the second aspect of neuronal responses, the noise, have not previously been studied. Spike counts of the responses of neocortical neurons to stimuli that are present for several hundred milliseconds are characteristically variable (Tolhurst et al., 1981; Tomko and Crapper, 1984; Snowden et al., 1992), far more so than the responses of some peripheral neurons (e.g., Matthews and Stein, 1969; Whitsel et al., 1977). The source of the variability is unknown. It may result from several sources, including synaptic processes, cyclical changes resulting from slow-wave activity in the brain, or changes in the response characteristics of individual neurons (Tomko and Crapper, 1984; Softky and Koch, 1993; Shadlen and Newsome, 1995, 1998). Some studies have suggested that lower variance is found in alert animals compared to anesthetized animals, although the effects are typically small (Vogels et al., 1989; Snowden et al., 1992).

The variability of responses depends in a characteristic way on response magnitude. The variance of spike counts is typically proportional to the mean number of spikes produced by a stimulus (Henry et al., 1973; Heggelund and Albus, 1978; Dean, 1981; Tolhurst et al., 1981; Snowden et al., 1992; Britten et al., 1993; Geisler and Albrecht, 1997). Because noise (standard deviation) is the square root of variance, and variance is proportional to response (signal), increasing the response of a cortical neuron is expected to improve its signal-to-noise ratio. Further, the distribution of interspike intervals is generally well fit by an exponential distribution, as expected for a random (Poisson) process, suggesting that response variability might be an intrinsic feature of cortical neurons (Shadlen and Newsome, 1998). However, behavioral state might alter the variability of neurons. It is possible that attention might decrease variance associated with particular response magnitudes, thereby causing neuronal responses to become more reliable and enhance the discriminability of stimuli. Alternatively, attention might not change the variability of neuronal responses but by increasing responses would still increase the signal-to-noise ratio for the neuron.

To address how attention affects stimulus discriminability, we recorded the responses of neurons in area V4 of rhesus monkeys to stimuli that were either attended or ignored. We studied how attention affects the magnitude and the reliability of differences between responses to oriented stimuli and thereby alters the ability of neurons to discriminate orientations. Additionally, we explored whether attention affects the temporal pattern of sensory responses. The results suggest that the increased neuronal responsiveness associated with attention does not alter response variability but that the increased responsiveness by itself improves stimulus discriminability.

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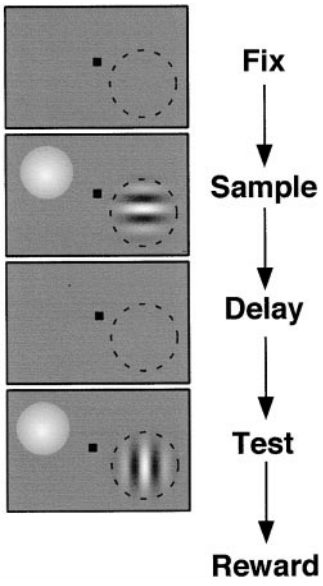

Figure 1. Delayed Match-to-Sample Task

Each frame represents the display at a different point in a trial. The fixation point is in the center of the screen and the neuron's receptive field is indicated by the dashed oval. The monkey was required to look at the fixation point and depress a lever to begin each trial. A Gabor and a colored Gaussian were shown during the sample period. The monkey attended to only one of the stimuli on each trial, depending upon previous instruction trials during which only one stimulus was presented in the sample and test periods. In the attended mode, the monkey was required to report whether the orientations of the sample and test Gabors in the receptive field were the same or different. In the unattended mode, the monkey was required to report whether the colors of the sample and test Gaussians outside the receptive field were the same or different.

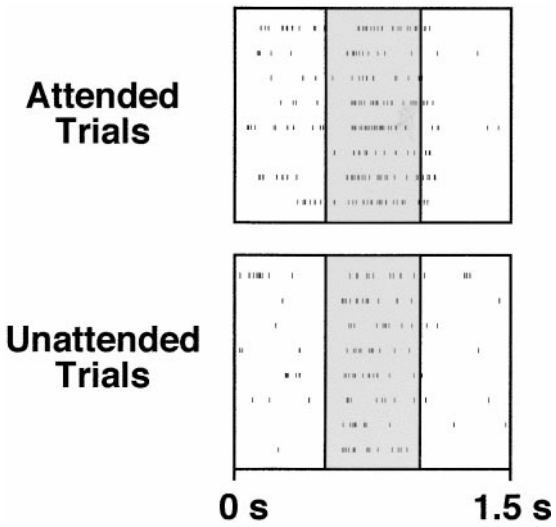

Figure 2. The Variability of Neuronal Responses

Each dot represents a single action potential. The x axis shows the time of the spike relative to the stimulus period (shaded portion). Each row along the y axis indicates a different trial. The upper rasters correspond to trials from the attended mode; the lower rasters correspond to trials from the unattended mode. Even in response to the same visual stimulation in the same behavioral condition, the neuron does not fire the same pattern or number of spikes.

Results

We recorded from individual neurons in two monkeys (*Macaca mulatta*) while they performed a delayed match-to-sample task with two modes (Figure 1). Details of the task are in the Experimental Procedures. Briefly, the animals were required to maintain their gaze on a central spot of light throughout each trial and to report, using a lever, whether the stimuli appearing sequentially in the same location were the same or different. The animal was either required to report whether the sample and test orientations matched when attending to the oriented stimuli or to report whether the sample and test colors matched when attending to the colored stimuli. We define an attention difference with respect to whether the stimulus in the receptive field of the neuron being recorded from was relevant or irrelevant to the current task that the animal was performing. The oriented stimuli were always placed in the receptive field of the neuron being recorded, and the colored stimuli were always placed outside that neuron's receptive field. Thus, when the animal performed the orientation matching task, the neuron being recorded from was responding to the relevant stimulus, and we refer to this as the "attended" mode. When the animal performed the color matching task, that neuron was still responding to the grating patch, but because this stimulus was now irrelevant to the animal's task, we refer to this as the "unattended" mode.

We obtained data from 262 neurons in area V4. Each cell was tested with at least 8 presentations of each of 12 orientations in both modes. All data analysis was restricted to the sample stimulus presentation period during which the retinal stimulation was the same in both modes. The effects of attention on the strength of neuronal responses, the width of orientation tuning curves, and the undriven activity of these neurons have been reported elsewhere (McAdams and Maunsell, 1999). Briefly, 85% of the neurons (223/262) had significant modulation of their responses depending on the orientation of the sample stimulus, and 55% of the neurons (145/262) had significant modulations depending on which stimuli the animal was required to attend to (two-factor ANOVA, $p < 0.05$). Neurons with significant effects for both orientation and attention made up 47% (122/262) of the neurons, consistent with these properties occurring independently. Most of the significant effects of attention were increased firing rates in the attended condition (86%, 125/145). Here, we consider how attention affects the variability and discriminability of neuronal signals.

Response Variability

Rasters of the neuronal responses from one neuron for many repetitions of the preferred orientation of a grating patch in the attended and unattended conditions are shown in Figure 2. Even for the same stimulus and behavioral conditions, both the total number of spikes and the time at which they occur varies from trial to trial. Nevertheless, the neuron tended to produce more

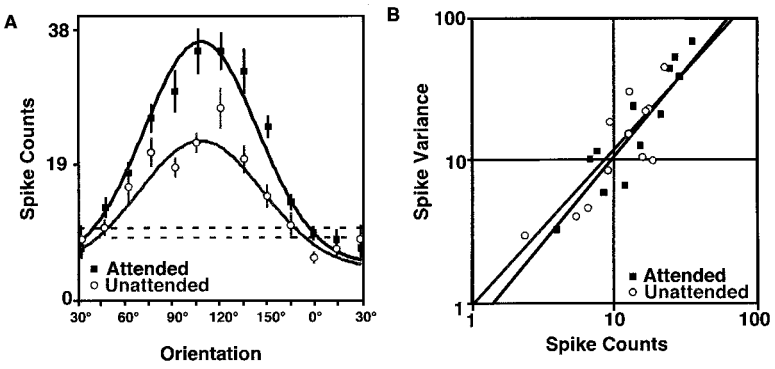

Figure 3. Tuning Curves and Response Variance Functions from a Single Neuron

(A) The orientation tuning curves for the attended (closed squares) and unattended (open circles) modes are shown for a single neuron. Each point is the mean spike counts ± the standard error bars. The dashed lines indicate the undriven activity of the neuron during each behavioral mode, determined from the activity of the neuron during the fixation period, before a visual stimulus is presented in the receptive field of the cell. This cell has a 73% increase in the amplitude of its tuning function by attention.

(B) The spike counts are plotted against the variance of the spike counts for each orientation in each behavioral mode. Power functions are fit to the responses for each behavioral mode. The two power functions are not significantly different (power: attended, 1.2; unattended, 1.1; coefficient: attended, 0.02; unattended, 0.08).

spikes overall when the animal was attending to this stimulus (attended mode, 58 spikes/s; unattended mode, 37 spikes/s). Does attention alter the variability of neuronal firing as well?

We addressed this issue by determining whether the realtionship between response magnitude and response variance differs between the attended and unattended modes of the task for single neurons. Each cell was tested with a range of orientations that produced a range of mean spike counts. These were used to examine the relationship between the mean counts and the variance of counts. An example is shown in Figure 3, using additional data from the neuron whose responses to its preferred orientation (105°) were shown in raster format in Figure 2. This neuron's responses were about 30% stronger regardless of stimulus orientation when the animal attended to the receptive field stimulus (amplitude of tuning function: attended mode, 50 spikes/s; unattended mode, 29 spikes/s; Mann-Whitney U test on amplitudes of the fitted tuning functions, $p < 0.05$). Figure 2B replots these data as mean spike counts against spike count variance (log axes). Data from the attended and unattended modes were fit with power functions, which have two terms, the power and the coefficient. The power reflects how the rate of rise of the function varies with the magnitude of the response, and the coefficient is a constant multiplier of the response magnitude. These functions are not significantly different (power, t test, $p > 0.5$; coefficient, t test, $p > 0.5$). Thus, there is no evidence that attention changed the relationship between mean spike counts and variance, although the overall mean spike counts did increase (attended points are shifted upward and to the right).

Across all cells recorded, the response variance functions had a median power of 0.85 in the unattended case and 0.89 in the attended case. The median coefficient in the attended mode was 1.64 and the median coefficient in the unattended mode was 1.80. These differences were not significant. Only 5% of cells (14/262) had significant differences in power (t test, $p < 0.05$), and only 12% of cells (30/248) had significant differences in coefficient (t test, $p < 0.05$). These individual differences were evenly split between net decreases and increases in variability by attention. The distributions of power and coefficient were also not significantly altered by attention (power, Wilcoxon signed rank test, $p > 0.80$; coefficient, Wilcoxon signed rank test, $p > 0.80$).

Because cortical neurons typically have similar response variance functions, with the fitted power generally being close to 1.0 (Heggelund and Albus, 1978; Tolhurst et al., 1981; Tomko and Crapper, 1984; Snowden et al. 1992; Geisler and Albrecht, 1997), another assessment of the effects of attention on the response variance of cortical neurons can be obtained by pooling data across neurons. Population response variance fits were made by pooling the responses versus their variance for each visual stimulus across all neurons in area V4 for each task mode. These composite data were fit with power functions for each condition and are plotted for the attended mode (Figure 4A) and the unattended mode (Figure 4B). These fits to the population data are not significantly different (power, t test, $p > 0.05$; coefficient, t test, $p > 0.05$). Under our task conditions, there was no evidence that attention alters the overall relationship between response magnitude and variability.

Response Discriminability

Although attention did not alter the relationship between mean response and variance, it did increase the rate of firing (e.g., Figure 3A). This increase in responsiveness could by itself affect signal discriminability. We used the functions that describe the orientation tuning and variability of each neuron to analyze how well each neuron could discriminate orientation, as illustrated in Figure 5. In Figure 5A, one half of the orientation tuning curves for the attended and unattended modes from an exemplar neuron are plotted. In either mode, the ability of the neuron to discriminate two orientations depends in part on the magnitude of the difference in the responses to various orientations. This difference is captured by the slopes of the orientation tuning functions, which are plotted in Figure 5B. The slope is greatest on the flanks of the tuning curves. The greater amplitude

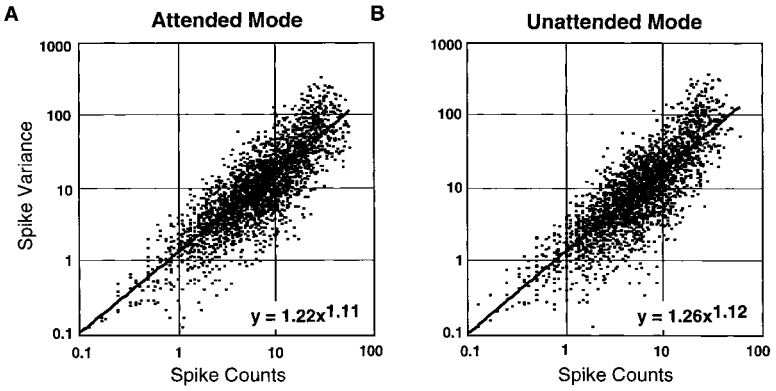

Figure 4. Population Response Variance Functions

These response variance functions were constructed by fitting power functions to the response variance data from all of the V4 neurons. The two functions are not significantly different (power: attended, 1.11; unattended, 1.12; coefficient: attended, 1.22; unattended, 1.26).

in the attended mode tuning curve results in a correspondingly greater slope.

The variability of the responses also affects the ability of the neuron to signal a particular orientation and therefore to signal differences between orientations. Because variance is typically proportional to mean response, the standard deviation (SD), which is the square root of variance, increases approximately as the square root of the response. In Figure 5C, the relationship between SD and the response is shown, calculated as the square root of the best-fitting response variance function. This neuron, like most neurons recorded, did not show any significant difference in the fitted response variance function for the attended mode compared to the unattended mode. The data have therefore been fit with a single curve. The logarithmic increase of SD (noise) with mean response (signal) causes the neuron's signal-to-noise ratio to improve at higher firing rates. This result has been shown previously in experiments in anesthetized animals using different stimulus parameters to alter response rate (Tolhurst et al., 1983; Snowden et al., 1992). To relate the effects of mean response and its SD to orientation tuning curves, the SDs of the response to different orientations are plotted in Figure 5D for the attended and unattended conditions. The curves in this plot are derived from the two fitted curves in Figure 5A and the single function in Figure 5C.

The ability of a neuron to discriminate changes around a given orientation can be estimated by a signal-to-noise ratio that relates the slope of the orientation tuning curve ("signal" about orientation difference, Figure 5B) to the SD of responses ("noise," Figure 5D). This ratio, a d' measure (see Experimental Procedures), is plotted as a function of orientation in Figure 5E. This function corresponds to the difference in orientation needed to make this neuron produce responses that differed by one SD of the response. This value varies considerably with orientation. Smaller d' values indicate a better ability to discriminate. As noted by Scobey and Gabor (1989), this function has a long, broad minimum that covers much of the flank of the tuning function. It rises sharply where the slope of the tuning function approaches zero. We defined the best discriminability of the neuron for each task mode as the minimum of this function. For the responses shown in Figure 5E, the best discriminability was 10° in the attended mode and 14° in the unattended mode.

Figure 6 plots the best discriminability in the attended condition against the best discriminability in the unattended condition for all V4 neurons recorded. If attention had no systemic effect on the ability of neurons to signal orientation changes, the points would be symmetrically distributed about the diagonal. More points fall below the diagonal, showing that attention improves the ability of these neurons to discriminate orientations (Wilcoxon signed rank test, $p < 0.001$), albeit modestly. The median discriminability value for the attended mode is 20.4°, and the median discriminability value for the unattended mode is 26.5°.

We also used receiver operating characteristic (ROC) analysis to assess the effects of attention on orientation discriminability (see Experimental Procedures). ROC analysis is a direct comparison of the probability that two response distributions overlap. We used this analysis to confirm the results of the previous analysis, which depended on modeling both the tuning functions and the response variance functions. Although the data from specific cells was slightly different depending on the analysis method, the overall population data was very similar. For the population, the median ROC discriminability values were 14.5° in the attended mode and 19.6° in the unattended mode (Wilcoxon signed rank test, $p < 0.001$). Thus, the two analysis techniques produced very similar results with a median 6° improvement in orientation discriminability using the first method and a median 5° improvement using ROC analysis.

Population Summary

In the previous section, we reported that attention causes small improvements in the orientation discriminability of single cells. However, visual information can be integrated by pooling the responses from many cells. We assessed the potential effects of pooling by examining how the number of neurons whose discriminability performance reached a particular criterion varied with attention.

In Figure 7, a cumulative plot of the proportion of cells whose best orientation discriminability was at or below the particular orientation discriminability values on the x is are shown for the attended and unattended modes. The two curves diverge as the proportion of cells increases. This suggests that the effects of attention on orientation discriminability are independent of the selectivity of the cell for orientation, consistent with our previous report on the tuning of these cells (McAdams and

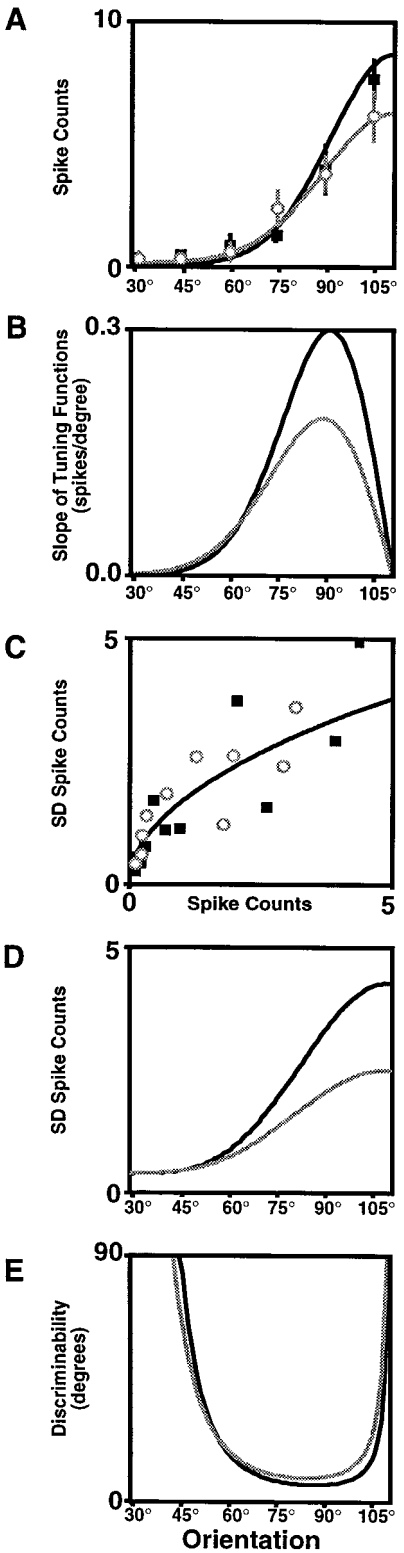

Figure 5. Discriminability Calculations

Details are in the text.

(A) Half of the responses and the fitted tuning functions for the attended (black) and unattended (gray) conditions.

(B) Half of the slope of the fitted tuning functions for each task mode.

(C) The response-noise function for this neuron. Only one function is shown because the two behavioral modes were not significantly different.

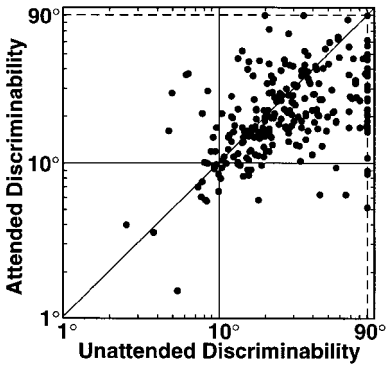

Figure 6. Orientation Discriminability Values

The best discriminability in the attended mode is plotted against the best discriminability in the unattended mode for all neurons. Points falling along the diagonal show no change in discriminability by attention. The dashed lines at 90° indicate the limit of meaningful discriminability values. Many points approach this limit in the unattended mode, but only a few in the attended mode.

Maunsell, 1999). Neither the attended curve nor the unattended curve reach 100% at the maximal orientation discriminability value (90°) because not all cells reached our criterion for orientation discriminability. These cells were either poorly tuned to orientation or had very variable responses. A greater percentage of neurons do not reach criterion in the unattended mode than in the attended mode, suggesting that attention may increase the percentage of neurons contributing to orientation discriminability in cortical area V4.

Temporal Coding

Neurons might transmit information using both the rate of spiking and the relative intervals between single spikes (Legendy and Salcman, 1985; Richmond and Optican, 1987; Singer and Gray, 1995; Victor and Purpura, 1996). In auditory cortex, the timing of spikes conveys considerable information about the particular stimulus (Carney and Yin, 1988; deCharms and Merzenich, 1996). As attention appears to increase the amount of information that reaches perception (Rensink et al., 1997), this result could be due to either a change in spike rate or a more specific change in the relative timing of the spikes. In the previous sections, we demonstrated that the increase in response by attention improves the discriminability of orientations using the spike rates of single neurons. In this section, we examine whether attention changed the relative timing of spikes.

One question is whether attention makes neurons more likely to fire spikes in bursts. We consider bursts to be short periods of time of elevated firing rate. Strehler and Lestienne (1989) have suggested that the bursting of neurons might be important in neuronal signaling, as a pair or triplet of spikes may be more effective in driving neurons. Attention might make neurons more likely to

(D) The noise predicted for each orientation along the tuning function.

(E) The discriminability of the neuron at each orientation.

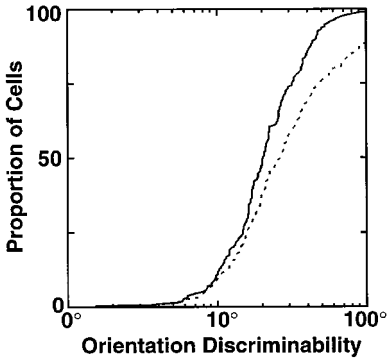

Figure 7. Changes in the Discriminability Threshold in the Population

This is a cumulative plot, showing the proportion of cells achieving a given orientation discriminability value. The solid line indicates the data obtained from the attended mode; the dashed line indicates the data obtained from the unattended mode. A greater proportion of cells contributes to orientation discriminability in the attended mode than in the unattended mode.

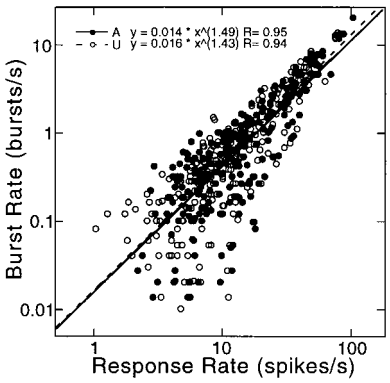

Figure 8. The Effect of Attention on the Frequency of Bursts

The burst rate is plotted against the response rate for the attended (closed symbols and solid line) and unattended (open symbols and dashed line) modes. The response-burst functions were constructed by fitting power functions to the data from all of the V4 neurons for each mode. Attention does not alter the relationship between response rate and burst rate.

fire bursts and thus become more effective at transmitting information. To ensure that our results did not depend upon the specific definition of bursts used, we performed analyses using several different criteria to define a burst (see Experimental Procedures). The basic technique involved scanning each spike train for spikes occurring with short interspike intervals. We varied the minimum length of the interspike intervals and the minimal number of spikes required to define a burst. We also performed each analysis in two ways, collapsing data from each neuron across orientations and taking each orientation as a separate data point. Cells or orientations that did not have any bursts by that criterion were excluded from each analysis.

Although attention caused a significant increase in response rate (median attended, 12.6 spikes/s; unattended, 10.7 spikes/s; Mann-Whitney U test, $p = 0.04$), it did not significantly change the rate of the bursts (median attended, 0.64 bursts/s; unattended, 0.50 bursts/s; $p = 0.08$), the number of spikes within each burst (median attended, 2.1 spikes/burst; unattended, 2.1 spikes/burst; Mann-Whitney U test, $p = 0.63$), or the length of each burst (median interspike interval attended, 4.0 ms; unattended, 4.0 ms; Mann-Whitney U test, $p = 0.64$), using a definition of a burst as a time period during the sample stimulus presentation in which two or more spikes occurred, with each interspike interval less than 5 ms and with responses collapsed across all orientations for each behavioral condition. With some of the criteria for defining bursts, we did find that attention caused statistically significant increases in the number of bursts and the rate of bursts. However, because attention increases the firing rate and an increased firing rate is associated with decreased interspike intervals, we needed to determine whether the relationship between the burst rate and response rate was altered by attention or whether the increased burst rate was simply a result of the increased responses. In Figure 8, we fit power functions to the burst rate versus the average response rate of the neuron. The functions are not significantly different (power, t test, $p > 0.05$; coefficient, t test, $p > 0.05$), suggesting that attention does not systematically alter the relationship between response and the tendency to produce bursts. Attention did not significantly alter this relationship for all 16 different analyses using 8 different temporal interval definitions of bursts.

Discussion

We have found that attention does not alter the relationship between mean response and response variance in V4 neurons. Other studies have demonstrated that various stimulus manipulations that drive a neuron at different firing rates do not change the variability associated with each firing rate. These include manipulations of contrast, spatial frequency, and speed and direction of motion (Dean, 1981; Tolhurst et al., 1983; Snowden et al., 1992). The variability of neuronal responses appears to be consistent throughout neocortex (Dean, 1981; Tolhurst et al., 1983; Bradley et al., 1987; Scobey and Gabor, 1989; Vogels et al., 1989; Snowden et al., 1992; Britten et al., 1993; Softky and Koch, 1993; Geisler and Albrecht, 1997) and may be a fundamental aspect of cortical processing (Shadlen and Newsome, 1998). We suggest that modulations relating to behavioral state are no different than sensory manipulations in their effects on response variability.

Although attention did not affect the relationship between neuronal response and variability, the ability of the neuron to signal a particular stimulus was improved by attention. Attention improved orientation discriminability of individual neurons (median change, 6°). This improvement can be attributed solely to the increase in response amplitude caused by attention, which effects discriminability in two ways. First, the amplitude change increased the slope of the tuning function, thereby producing larger differences in responses to orientations along the slope. Second, by moving responses to higher rates, the signal-to-noise ratio of the neuron is improved as the signal increases more rapidly than the noise.

These improvements in neural performance conferred by attention appear indistinguishable from those that would result from stimulus manipulations that increased responses a comparable amount.

The discriminability values we report, both for the attended and unattended modes, are considerably poorer than those reported in other studies of cortical neurons (Heggelund and Albus, 1978; Bradley et al., 1987; Scobey and Gabor, 1989; Geisler and Albrecht, 1997). In the most extreme cases, cortical neurons have been reported to have discrimination thresholds of less than 1°. Although a few of the V4 neurons approached this performance (Figure 6), most were far worse. Much of this difference can be explained by the relative weakness of the neuronal responses we analyzed, which came from several factors. First, V4 neurons are harder to drive than V1 neurons, and a simple stimulus is unlikely to be optimal (Tanaka et al., 1991; Gallant et al., 1993). We used an isoluminant, counterphasing Gabor of relatively low spatial frequency rather than a bright, static grating or bar to stimulate the neurons, because Gabor stimuli have relatively little high–spatial frequency content, which should decrease the effects of small eye movement during fixation on the neuronal response (Parker and Hawken, 1985; Shapley and Victor, 1986). Finally, if the stimulus was much smaller, or higher in spatial frequency, than the monkeys had become accustomed to working with, they occasionally refused to work with the best stimulus. This would further reduce the overall level of response. We knowingly used a nonoptimal spatial frequency or stimulus size for around 15% of the cells.

One interesting question is how the change at the neuronal level relates to the change in behavioral performance. Although the responses of the single V4 neurons we recorded appear to carry information about small orientation discriminations, our animals were not trained to report these fine orientation discriminations, and their orientation discrimination thresholds were not determined. Other studies in awake monkeys using square-wave gratings rather than Gabor patches have reported orientation discriminability thresholds ranging from 2° to 20° (Vogels and Orban, 1994; De Weerd et al., 1996). This wide range of orientation discriminability thresholds suggests that discriminability depends not only on the stimuli chosen but also on the specific task and the animal's cooperation and training. The effects of attention on the orientation discriminability of single units that we measured here are comparable to at least one estimate of the effects of attention on orientation discriminability in humans. Lee and his colleagues (1997) reported that attention decreased orientation discriminability thresholds by 2.9- to 5-fold, corresponding to absolute changes of about 3°–4° in a study which measured the orientation discriminability of sinusoidal gratings in an attended and unattended state in human observers.

The current results suggest that the behavioral modulations related to attention do not confer any special improvements in neural performance beyond those associated with stronger responses. This result extends a previous finding that attention does not change the sharpness of orientation tuning for V4 neurons (McAdams and Maunsell, 1999). Together, these results suggest that manipulations of behavioral state affect cortical responses in a way that may be equivalent to manipulations of sensory stimuli. It is possible that retinal and extraretinal inputs to cortical neurons employ similar circuits, cell types, and synaptic mechanisms and differ only in the information that they convey.

A simple increase in the gain of selected neuronal responses could explain the improvements in behavioral performance that are associated with attention. The neurophysiological consequences of attention mimic the effects of making a stimulus brighter or otherwise more salient, and behavioral performance for attended stimuli might be superior for the same reasons it is superior for more salient targets. Whether an effective increase in the salience of an object can account for all the behavioral improvements resulting from attention is an important question that remains to be addressed. Experiments that relate the magnitudes of single cell responses to behavioral performance across a range of stimulus and attentional conditions will be important in addressing this issue.

Experimental Procedures

Behavioral Paradigms

The animals performed a delayed match-to-sample task with two modes. Each trial began when the animal looked at the fixation point and depressed a lever. Sample stimuli then appeared simultaneously at two locations for 500 ms. Only one location was behaviorally relevant on a given trial. The stimuli were removed for 500 ms, then two test stimuli appeared, at which point the animal had to indicate whether the test stimulus at the relevant location matched the sample stimulus previously presented at that location. If the sample and test matched, the animal had to release a lever within 500 ms of the test stimulus onset to receive a reward. If they did not match, the animal had to keep the lever depressed for 750–1000 ms, after which he received a reward. The relevant location was cued to the animal by presenting instruction trials in which only one stimulus appeared. After the animal performed two instruction trials correctly, the second stimulus returned. He continued to direct his attention to the instructed location until new instruction trials were provided. One location was inside the receptive field of the neuron being recorded and the other location was outside the receptive field, diametrically opposed at the same eccentricity. When the animal's attention was directed to the oriented stimuli in the receptive field of the neuron being recorded, the neuron's responses could be relevant to the task the animal was performing and we refer to that condition as attended. When the animal's attention was directed to the colored stimuli outside the receptive field of the neuron being recorded, its responses would be irrelevant to the animal's task and we refer to that condition as unattended. Trials were aborted if the animal released the lever before the test stimuli appeared or broke fixation before completing each trial.

The stimuli in the receptive field were temporally sinusoidally (4 Hz) counterphasing Gabor patches; the stimuli outside the receptive field were colored patches with a two-dimensional Gaussian profile. Both stimuli were isoluminant on a gray background, to minimize any effects of small offsets in eye position that may have occurred across the two conditions. Because both animals were always required to maintain fixation within 0.7° of the fixation target center, differences in neuronal responses between the two types of trials can be attributed to differences in behavioral state rather than differences in the visual stimulation. Data analysis is restricted to the responses elicited during the presentation of the sample stimuli. During this period, the only difference between the attended and unattended modes is which stimulus and what information the animal is required to encode. The same visual stimulation is given and the animal has the same motor requirements (maintaining fixation on the central spot of light and keeping the lever depressed) for both conditions.

Neuronal Recording and Data Collection

Recordings were usually made daily during a 3–5 week session primarily using transdural recordings with Pt/Ir recording electrodes of 1–2 MΩ at 1 kHz (Wolbarsht et al., 1960). A small fraction of the data (30/262 cells) was recorded from the parts of V4 in the superior temporal sulcus using guidetubes with similar electrodes. Signals from the microelectrode were amplified, filtered, and monitored on an oscilloscope and audio monitor using conventional equipment.

The animal performed the match-to-sample task while we searched for units. Units were isolated on the basis of waveform, with the requirement that the peak of the action potential be at least three times the background noise. When a unit was isolated, its receptive field was mapped with a bar moved by hand while the animal fixated a small spot of light. The grating patches were then adjusted in spatial frequency, color, and size to yield the best response using the match-to-sample task, as judged by listening to the audio monitor. Once stimulus parameters were set, they were used for all data collected from the neuron. The stimuli in the receptive field were temporally sinusoidally (4 Hz) counterphasing Gabor patches; the stimuli outside the receptive field were colored patches with a two-dimensional Gaussian profile. Both stimuli were isoluminant on a gray background, to minimize any effects of small offsets in eye position that may have occurred across the two conditions.

Data Analysis

We measured neuronal responses during the presentation of the sample stimulus. We collected at least 8 repetitions of 12 orientations in each of the two task modes, where task mode is defined by whether the animal attended to the stimulus inside (attended mode) or outside (unattended mode) the receptive field. Only correctly completed trials, excluding instruction trials, were counted and used in data analysis. Task mode alternated after obtaining two repetitions of each of the twelve orientations.

Orientation tuning curves were constructed by fitting the responses for each orientation with a Gaussian using a nonlinear least-squares optimization procedure (see McAdams and Maunsell, 1999). Two tuning curves were fit for each neuron: one corresponding to the responses collected during the attended state and the other corresponding to the responses obtained during the unattended state. Response variance functions were made by fitting the logarithm of the average spike counts against the logarithm of the variance of those spike counts with a linear regression to obtain a slope (power) and an intercept (coefficient). Significant differences in the two curves were determined by comparing the slopes and intercepts of the simple linear regression equations, using modified t tests (Zar, 1984). If the fitted parameters did not differ significantly, a single response variance function was obtained for the neuron by collapsing the data sets for the two conditions.

We used ideal observer theory to compute the best possible performance given the recorded neuronal responses. We used two slightly different methods to implement ideal observer theory. Both methods involved a calculation of orientation difference by which two stimuli would have to be separated in order for the neuronal responses to the two to be discriminated at a certain level of performance. A common measure of ability to signal differences is determined by dividing the responses to two stimuli by the standard deviation associated with those responses: $d' = (R_1 - R_2)/SD_{(1,2)}$ (Equation 1).

If the stimuli eliciting responses one and two can be related by a particular function, as the difference in the two stimuli decreases to zero the numerator of equation one becomes the slope of that function at a particular orientation. The denominator is then the standard deviation associated with the response at that value. In this way, a discriminability function is calculated: d′(orientation) = slope(orientation)/SD(orientation) (Equation 2). We produced a discriminability curve for each task mode using the fitted Gaussians and fitted response variance functions (Scobey and Gabor, 1989; Geisler and Albrecht, 1997). We calculated d′ at each orientation by dividing the slope of the tuning function by the standard deviation corresponding to the response magnitude at that orientation, as estimated from the response variance function. When d′ is 1.0, the performance in a two-interval forced-choice task corresponds to 75% correct. Therefore, the reciprocal of our calculated d′ value corresponds to the number of degrees with which two orientations would be required to differ in order for those response distributions to be separable 75% of the time. We will refer to each neuron's best discriminability as the reciprocal of its minimal d′ value for each task mode.

We also used ROC analysis to confirm the results from descriptive function analysis (Green and Swets, 1966; Bradley et al., 1987). Like the descriptive-function approach, ROC analysis also calculates the best discriminability possible by the neuron but uses only the actual neuronal responses to pairs of specific stimuli rather than the fitted functions for its calculations. It involves comparing the responses produced by a given orientation with those from another orientation. The probability that an ideal observer could distinguish between a pair of response distributions was determined using a simple rule: if the response is above a criterion then the answer is one orientation, and if the response is below that criterion then the answer is the other orientation. The criterion was varied across the entire range of responses found in the two distributions. If the response distributions were completely nonoverlapping, any criterion between the maximal response of the orientation eliciting less response and the minimal response of the orientation eliciting more response will result in 100% discriminability or a probability of 1.0. Conversely, if the response distributions are identical, no criterion produces performance above chance. For each cell, the greatest probability for discriminating the response distributions was determined for each pair of stimuli. These probabilities were plotted against orientation difference. Then, the interpolated orientation difference at which the probability of distinguishing the orientations exceeded a threshold of 75% was taken as the discriminability threshold of the cell. We defined the best ROC discriminability for each condition as the minimal threshold obtained among all orientations tested for each mode.

Finally, we tested whether attention affected the number of bursts of spikes that cells fire. A burst is a brief period of increased firing rate. We tried several different definitions of bursts to ensure that our results were not dependent on the specific intervals chosen. The simplest definition was two spikes occurring during the same stimulus presentation with an interspike interval less than a specified amount. We used intervals of 3 ms, 5 ms, 8 ms, and 10 ms, which correspond to firing rates of 333 Hz, 200 Hz, 125 Hz, and 100 Hz. We repeated the analyses with the additional requirement that a third spike occur with an interspike interval of no more than 15 ms. Each analysis was done first with the data collapsed across all orientations and then again using each orientation as a separate data point. Thus, a total of 16 different analyses were performed, using 8 different definitions of bursts. Cells or conditions in which no bursts were identified were excluded from the statistical analysis. The significance of the data was assessed as a population using Mann-Whitney U tests to determine if attention affected the firing rate, the number of bursts, the number of spikes in each burst, and the length of each burst. Additionally, the relationship between response rate and burst rate was assessed by comparing the linear regression equations for the attended and unattended states, using modified t tests on the slopes and intercepts (Zar, 1984).

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