

# Attention Increases Sensitivity of V4 Neurons

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## Summary

When attention is directed to a location in the visual field, sensitivity to stimuli at that location is increased. At the neuronal level, this could arise either through a multiplicative increase in firing rate or through an increase in the effective strength of the stimulus. To test conflicting predictions of these alternative models, we recorded responses of V4 neurons to stimuli across a range of luminance contrasts and measured the change in response when monkeys attended to them in order to discriminate a target stimulus from nontargets. Attention caused greater increases in response at low contrast than at high contrast, consistent with an increase in effective stimulus strength. On average, attention increased the effective contrast of the attended stimulus by a factor of 1.51, an increase of 51% of its physical contrast.

## Introduction

Human behavioral studies of attention can be divided into two broad classes. Some studies have investigated *attentional selection*: the role of attention in selecting an individual target stimulus out of an array of competing stimuli (see, e.g., Treisman, 1980; Duncan and Humphreys, 1989; Wolfe, 1989). Other studies have probed *attentional facilitation*: the improved processing of a single stimulus when it appears alone at an attended location (see, e.g., Bashinski and Bacharach, 1980; Posner et al., 1980; Downing, 1988; Hawkins et al., 1990; Reinitz, 1990; Muller and Humphreys, 1991; Luck et al., 1994; Lee et al., 1997; Lu and Doshier, 1998). Recordings from neurons within the ventral processing stream in the visual cortex of macaque monkeys revealed a direct neural correlate of attentional selection. When multiple competing stimuli appear within the receptive fields of these neurons, their responses are determined primarily by the attended stimulus, and the influence of ignored stimuli is effectively filtered out of the neuronal signal (Moran and Desimone, 1985; Luck, et al., 1997; Reynolds, et al., 1999).

It has proven more difficult to find a consistent neural correlate of attentional facilitation in the ventral visual-processing stream. According to one proposal, attention

increases the magnitude of the neuronal response elicited by a single stimulus within the receptive field. Such a multiplicative increase in firing rate would be expected to improve stimulus detection by increasing the separation between stimulus-evoked responses and the neuron's spontaneous activity. It would also be expected to improve a neuron's ability to discriminate one stimulus from another. Consistent with this proposal, a number of studies in macaque area V4 have found increases in neuronal responses to attended stimuli (Spitzer et al., 1988; Connor et al., 1996, 1997; McAdams and Maunsell, 1999a, 1999b). However, other studies in area V4 have failed to find increases in the neuronal response when attention is directed to a single stimulus (Moran and Desimone, 1985; Haenny et al., 1988; Maunsell et al., 1991; Motter, 1993; Luck et al., 1997).

One possible explanation for the variability of attentional effects with a single stimulus within the receptive field is that attention increases neuronal sensitivity, but that the effect of attention on firing rate depends on where the stimulus falls on the contrast–response function. For example, an increase in sensitivity would not be expected to result in an increase in firing rate for high-contrast stimuli that are already at the saturation point on the contrast–response function. Evidence of such an increase in neuronal sensitivity would be a leftward shift in the neuronal contrast–response function when stimuli are attended. This proposal is illustrated in Figure 1A, which shows the contrast–response function of a hypothetical V4 neuron when attention is directed away from the neuron's receptive field (gray line). Cortical contrast–response functions are typically sigmoidal in shape, with increases in response being observed over a range of contrasts (shaded area) that comprise the dynamic range of the contrast–response function (Maffei and Fiorentini, 1973; Dean, 1981; Tolhurst et al., 1981; Albrecht and Hamilton, 1982). A leftward shift in the contrast–response function (solid black line) would be expected to cause larger increases in response for stimuli at or just below the dynamic range of the function. This is illustrated by the dashed line in Figure 1A, which shows the percent increase in response (indicated on the right axis) resulting from the indicated leftward shift in the contrast–response function. The change in firing rate (in spikes per second) is also predicted to peak within the dynamic range, as indicated by the dotted line, which shows the predicted increase in firing rate with attention as a function of contrast. The contrast–response function is plotted as a function of the logarithm of contrast. Therefore, a lateral shift in the function corresponds to a multiplication of the contrast necessary to reach a given level of response. Hence, we refer to this model as the *contrast gain model*.

By comparison, if attention causes a multiplicative increase in firing rate, then this increase should scale with firing rate, as illustrated in Figure 1B. Here, the neuronal response (above baseline) is multiplied by a constant gain factor, resulting in increases in firing rate with attention that grow larger with contrast. Because this model assumes that attention multiplies neuronal

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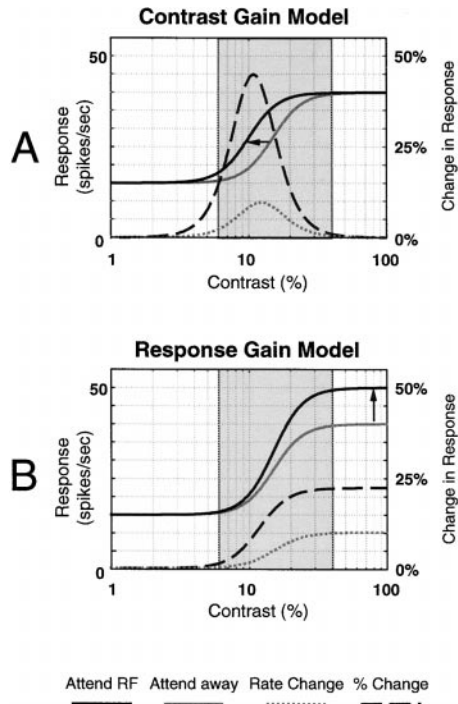


Figure 1. Two Models of How Attention Might Modulate a Neuron's Contrast-Response Function

(A) Contrast gain model. Attention causes a leftward shift in the contrast-response function. The gray curve represents the contrast-response function of a hypothetical neuron when attention is directed away from its receptive field. The black line represents the contrast-response function of the same neuron when attention is directed toward the receptive field. The largest changes in firing rate are predicted to occur for stimuli at or just below the dynamic range of the contrast-response function (shaded region). Responses are predicted to occur for stimuli just below the dynamic range, when they are attended. The percentage increase in firing rate (dashed line) is predicted to be greatest for stimuli near the bottom of the dynamic range. The increase in firing rate (in spikes per second, dotted line) is also predicted to peak within the dynamic range.

(B) Response gain model. Attention multiplies firing rate above baseline by a constant gain factor. The gray curve is identical to the curve in the upper panel. Attention multiplies the neuron's response above baseline at each contrast by a gain factor (black line). The largest change in firing rate (in spikes per second) is predicted to occur for stimuli of high contrast (dotted line), as is the largest percentage change in firing rate (dashed line).

firing rates, we will refer to it as the *response gain model*. In the present study, we distinguish between these alternatives by measuring the contrast-response functions of V4 neurons when the monkey either attended away from or toward the stimulus appearing within the receptive field.

## Results

We recorded responses of 84 well-isolated V4 neurons in two *Macaca mulatta* monkeys (40 neurons in one monkey, 44 neurons in the other) as they performed an attention-demanding task, and measured changes in neuronal responses with attention as a function of luminance contrast. The behavioral task we used to control

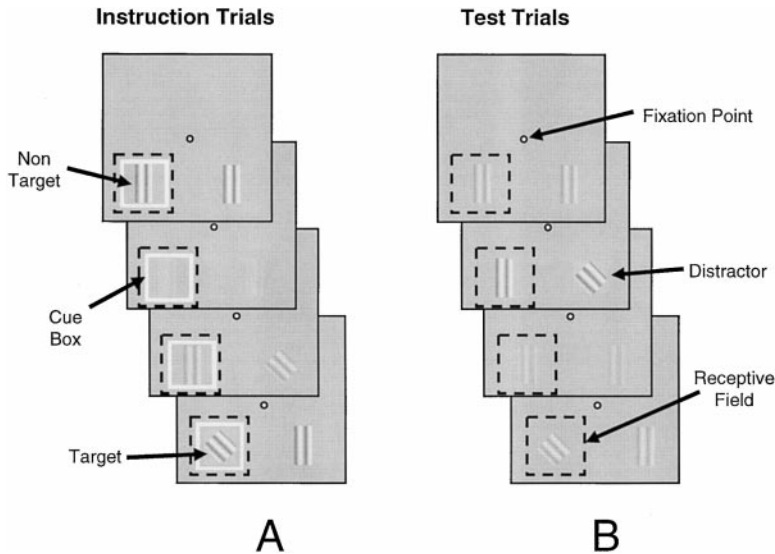
attention is similar to the task used by Luck et al. (1997) and is described in detail in the Experimental Procedures. Briefly, a monkey fixated a small spot of light at the center of a computer screen throughout each trial. Stimuli appeared at two locations: one inside the receptive field of the neuron being recorded, and another across the vertical meridian, at a position of equal eccentricity (see Figure 2). At the beginning of a block of trials, a few instruction trials were presented that indicated which of the two positions was to be attended during the remainder of the block. The monkey was required to quickly release a bar when a target stimulus appeared at the cued location. The target appeared at the end of a variable-length sequence of nontarget stimuli, and distractor targets occasionally appeared in the sequence of stimuli at the opposite location. Once the monkey was reliably responding to the targets appearing at the cued location and ignoring distractor targets at the uncued location, the cue was removed and the monkey had to continue to perform the task in the absence of the cue.

We measured neuronal responses to the identical stimuli appearing in the receptive field, when the monkey either attended to them or else attended to the stimuli appearing in the opposite hemifield. The luminance contrast of each stimulus was selected at random from a set of five contrasts that spanned the dynamic range of each neuron's contrast-response function, and thus the effects of attention could be measured for a given neuron at each point along the contrast-response function. By randomizing the contrast of both targets and nontargets, we ensured that the monkeys could not predict the contrast of the target in advance and adjust their attentional effort accordingly.

One of the two models we were considering (the contrast gain model) predicted diminished increases in firing rate with attention at high contrast. It was important to ensure that we would not observe such diminished increases in response at high contrast simply because our stimuli drove neurons to their maximum possible physiological firing rate, where no further increase would be possible. Therefore, we specifically selected stimuli that were not of the neuron's optimal orientation and spatial frequency, and would not, therefore, drive the neuron to its maximum possible firing rate. (See the Experimental Procedures for a complete description of how contrast, orientation, and spatial frequency were chosen.)

## Behavioral Performance

A total of 8.5% of all trials were terminated by premature eye movements, which did not appear to be related to the contrast of the target on a given trial. The monkeys responded inappropriately to the high-contrast distractor "foil" target at the unattended location on only 3% of the trials, compared to over 80% correct detection of the high-contrast target at the attended location, indicating that the monkeys attended to the correct location on nearly all trials. The task was demanding, as indicated by the fact that performance steadily declined with reduced target contrast. Excluding trials in which the monkey broke fixation, correct performance was, on average, 81.2% at the highest contrast and 77.4%, 72.5%,



**Figure 2. Stimulus Configuration and Task**  
The monkey fixated a small dot at the center of the computer screen. Sequences of oriented, bar-shaped patches of grating were simultaneously presented at two locations: one at the hot spot of the V4 receptive field (RF indicated by dashed black square) and the other at an equally eccentric position in the opposite hemifield. At the beginning of a block of trials, a white cue box appeared at one of the locations, to indicate which sequence should be attended. On each trial, variable-length sequences of stimuli appeared simultaneously at the two locations, and the monkey's task was to release a bar when it detected a target stimulus (a rotated square patch of grating) that appeared at the cued location. Once the monkey was responding reliably to the appearance of the target and ignoring distractor targets that occasionally appeared at the uncued location, the cue was removed, and the monkey had to continue to attend to the cued location throughout the rest of the trials. On each trial,

the length of the sequence was chosen at random to be from one to six stimuli. The contrast of each stimulus in the sequence was chosen at random. Therefore, the monkey could not predict when the target would appear and could not predict the contrast of a stimulus before it appeared.

69.8%, and 21.8% at successively lower target contrasts. This decrease in performance at low contrast resulted from an increase in the number of error trials in which the monkey never released the bar when the target appeared. The percentage of no-release trials increased from 8% on high-contrast trials up to 75.2% at the lowest contrast tested. The percentage of trials on which the monkey released prior to the appearance of the target (7.5%) did not depend on the contrast of the target.

### Neuronal Selectivity

As indicated above, it was important that the nontarget stimulus did not drive the neuron to its maximum possible firing rate. Therefore, during the initial mapping procedure, we tried to identify a stimulus that elicited a response that, while clear, was smaller than the response elicited by the neuron's preferred stimulus. We used this nonoptimal stimulus as the nontarget stimulus. Then, in the main experiment, we included probe trials in which the preferred stimulus appeared instead of the nontarget stimulus, while the monkey performed the attention task at the position opposite the receptive field. Thirty-nine of the 84 neurons (46%) had significantly different responses (computed over the 400 ms period following stimulus onset) to the preferred stimulus and the nontarget stimulus (unpaired t test,  $p < 0.01$ ) at high contrast. For these cells, the preferred stimulus elicited a response that was, on average, 65% higher than the nontarget stimulus. Across the entire population of 84 neurons, the response elicited by the preferred stimulus was, on average, 29% greater than the response elicited by the nontarget stimulus. The difference in response between preferred and nontarget stimuli was highly statistically significant (paired t test,  $p < 0.0001$ ). Thus, neurons were not being driven to their maximum physiological firing rate at high contrast.

### Population Average Responses

The response gain model predicted that the effects of attention should increase with firing rate, and, therefore, stimulus contrast, but this prediction was not supported by the data. Rather, the effects of attention on firing rates were greatest at low contrast (low firing rates) and smallest at high contrast (high firing rates), consistent with the contrast gain model. This is illustrated in Figure 3, which shows an example of a neuron tested at five contrast levels, when attention was either directed away from the stimulus in the receptive field (left column) or toward it (middle column). The average response of the neuron over time at each level of contrast is shown in the right column. There was no effect of attention on firing rate to the stimulus of 40% contrast (mean responses  $28.0 \pm 1.2$  SEM versus  $29.3 \pm 1.4$  SEM with and without attention, two-tailed t test,  $p = 0.49$ ) or 80% contrast (mean responses  $39.6 \pm 1.9$  SEM versus  $37.9 \pm 1.6$  SEM with and without attention, two-tailed t test,  $p = 0.51$ ), averaged over the 400 ms after stimulus onset. At 20% contrast there was a statistically significant (two-tailed t test,  $p = 0.007$ ) increase in response with attention, from  $27.5 \pm 1.4$  SEM spikes per second to  $33.7 \pm 1.6$  SEM spikes per second. The largest change in firing rate with attention was observed with the 10% contrast stimulus, which did not elicit a significant response when it was unattended and was thus below the neuron's contrast-response threshold (mean response during 400 ms after stimulus onset  $13.5 \pm 1.4$  SEM versus mean baseline response  $12.3 \pm 0.7$  SEM spikes per second, one-tailed t test,  $p = 0.26$ ). With attention to this subthreshold stimulus, the firing rate increased from  $13.5 \pm 1.4$  SEM spikes per second to  $23.1 \pm 1.5$  SEM spikes per second, which was highly significant (two-tailed t test,  $p = 0.00001$ ). Thus, attention reduced the contrast-response threshold of the neuron while having no effect on the response to high-contrast stimuli.

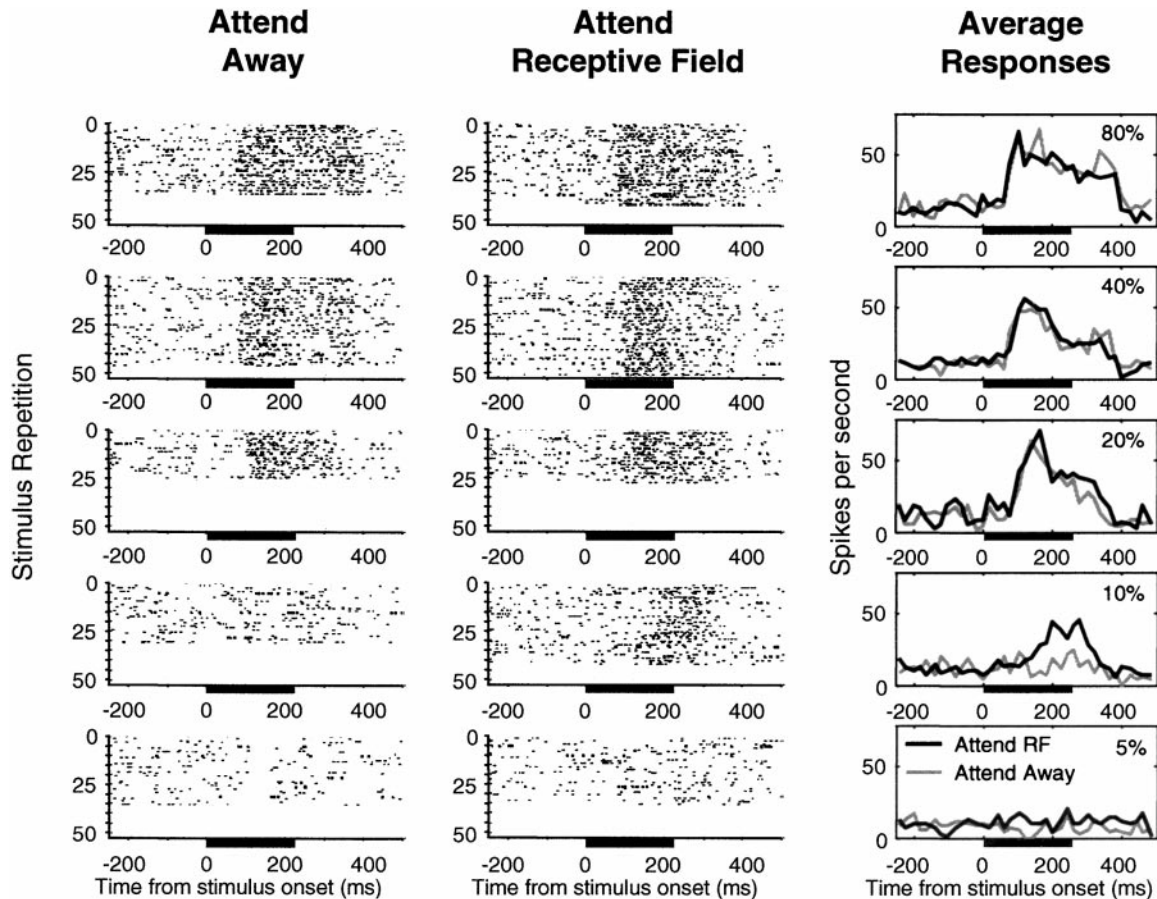


Figure 3. A Representative Neuron

The first two columns show the responses of a single neuron to a nontarget stimulus presented at five contrasts when attention was either directed away from the receptive field (left column) or toward it (middle column). Stimulus contrasts are arranged from the lowest contrast tested (5%) at the bottom up to the highest contrast tested (80%) on top. Each row corresponds to a single stimulus repetition, and each tick mark indicates an individual spike. Responses are aligned to the time of stimulus onset (0 ms), and the thick black line at the bottom of each panel shows the duration of the stimulus (250 ms). The right column shows the average response over time elicited when the stimulus in the receptive field was ignored (gray line) or attended (black line), binned at 20 ms resolution. Attention had no effect on the responses to 40% and 80% contrast gratings. Attention caused a small but significant increase in response at 20% contrast. The neuron did not respond to an unattended 10% contrast grating, but it responded clearly to the same stimulus when it was attended. Note that some raster plots have fewer rows than others. To maintain a constant raster marker size, we inserted blank rows so that each raster plot has 53 rows.

We observed smaller increases in firing rate with attention at high contrast across the population, as illustrated in Figure 4, which shows average responses of the entire population of 84 neurons. Attention caused the largest increases in firing rate to stimuli that were near the contrast-response threshold (the second lowest contrast tested, second panel from left). Here, attention caused a 24% increase in the average absolute firing rate (i.e., firing rate without subtracting away spontaneous activity) during the 400 ms after stimulus onset, and a 72% increase in the average response above baseline. A significant increase in firing rate with attention continued throughout the duration of the response ( $p < 0.001$ , paired *t* test). As stimulus contrast increased, the effects of attention on the neuronal response decreased. At the highest contrast tested, attention caused a 4% increase in absolute firing rate (9% increase in response above baseline), but this was not statistically significant (paired *t* test,  $p = 0.17$ ). For this highest contrast stimulus, there was no effect of attention during the initial 100–200 ms time period (paired *t*

test,  $p = 0.25$ ). However, there was a brief period late in the response, from 200 to 300 ms after stimulus onset, during which attention significantly (paired *t* test,  $p = 0.004$ ) increased absolute firing rate by 14% (25% increase in response above baseline). Consistent with observations in primary visual cortex (Gawne et al., 1996), response onset latency appears to increase at lower contrasts.

The effects of attention were reduced at high contrast both in terms of spikes per second and in terms of percent increases in firing rate. This is illustrated in Figure 5, which shows average responses to attended and ignored stimuli as a function of contrast. Figure 5A shows responses to attended (solid black line) and ignored (solid gray line) stimuli, averaged across neurons that were significantly modulated by attention, according to a two-way ANOVA (see Experimental Procedures).

Consistent with Luck et al. (1997), we found a small but statistically significant increase in spontaneous activity when monkeys attended to the receptive field location

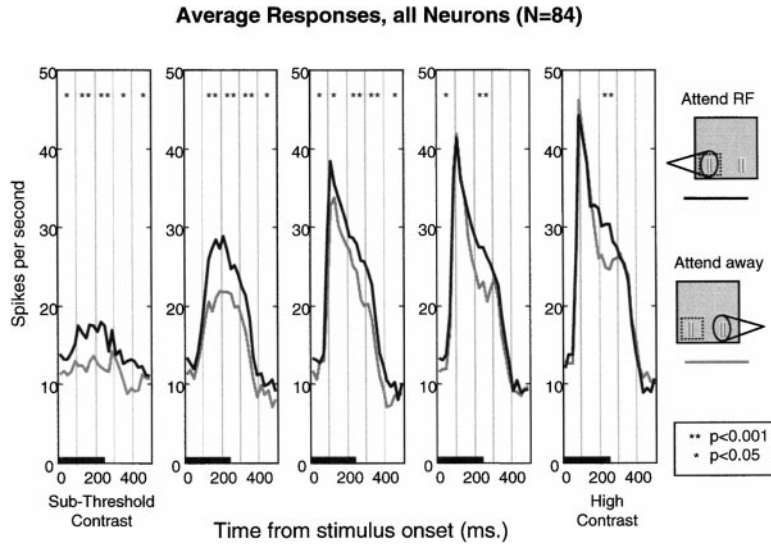


Figure 4. Timing and Magnitude of Attention Effects as a Function of Contrast

Each panel shows the response (in spikes per second) over time from the onset of the stimulus (in milliseconds) at a particular contrast, averaged across the entire population of 84 neurons. Dark bars at the lower left of each panel indicate stimulus duration (250 ms). The five panels are arranged according to contrast, from lowest (subthreshold) contrast on the left to highest (saturation) contrast on the right. Gray lines show average responses to ignored stimuli, when the monkey attended to the location that was across the vertical meridian from the receptive field. Black lines show responses to the identical stimulus when it was attended. The statistical significance of the attention effect within successive 100 ms periods is indicated by asterisks ( $p < 0.05$ ) and double asterisks ( $p < 0.001$ ) along the top of the figure. Responses are binned at 20 ms resolution.

in the absence of visual stimulation (0% contrast, left side of Figure 5A, mean spontaneous activity increases  $1.1 \pm 0.25$  SEM spikes per second, paired  $t$  test,  $p = 0.02$ ). As stimulus contrast was increased above threshold, the responses to attended and unattended stimuli separated and then converged again at saturation contrast. Thus, the largest increases in firing rate were observed at lower contrasts. This is indicated by the dashed line in Figure 5, which shows the percentage change in firing rate with attention, and the dotted line, which shows the change in firing rate in spikes per second. The lowest contrast tested showed the largest percent increase in firing rate (34%). As indicated above, the lowest contrast stimulus was chosen to be below the neuron's contrast-response threshold and therefore did not elicit a significant response when monkeys attended away from the receptive field. However, with attention to the receptive field, the average response to these subthreshold stimuli was significantly above baseline activity (mean increase in response  $5.9 \pm 0.9$  SEM spikes per second,  $p < 0.001$ , paired  $t$  test). This reduction in contrast-response threshold is consistent with a leftward shift in the contrast-response function, i.e., with the contrast gain model.

The increase in firing rate with attention diminished as a function of contrast, reaching a low of 3% at the highest contrast tested. This difference in firing rate between attended and unattended conditions was not statistically significant when the responses were averaged over the entire 400 ms period (mean increase in response with attention,  $0.9 \pm 0.8$  SEM spikes per second, paired  $t$  test,  $p = 0.59$ ). However, as noted above, the increase in firing rate with attention to the high-contrast stimulus was mainly limited to a brief period late in the response, and during this period the difference in response was significant (see Figure 4). Figure 5B shows responses averaged across the remaining 45 neurons that were not significantly modulated by attention.

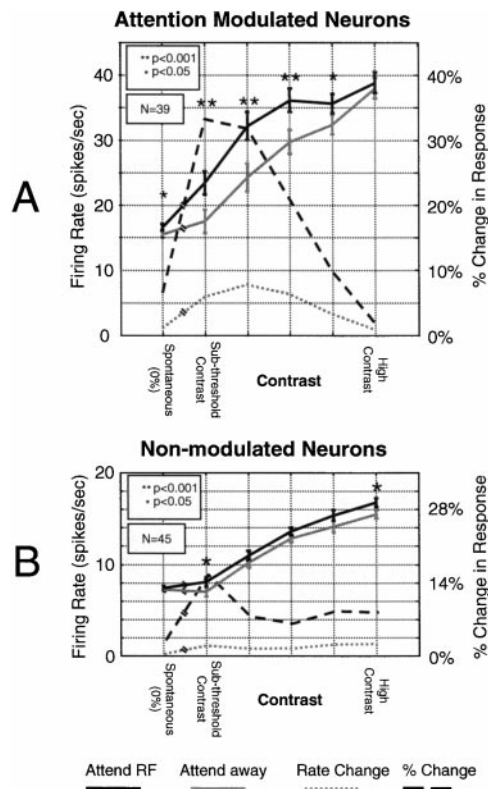
#### Attention Effects across Neurons

To verify that the larger increases in firing rate with attention at low contrast were typical of the population,

we separately computed the percentage change in response with attention for each neuron. The results are shown in Figure 6, in which frequency histograms show the distribution of changes in firing rate with attention across the population, at each level of contrast tested. Black and gray bars show the results for cells that were and were not significantly modulated by attention, respectively, according to a two-way ANOVA (see Experimental Procedures). Consistent with the results observed in the population average response, there were moderate increases in neurons' spontaneous firing rates (median 8.6% increase). Attention caused substantial increases in the response elicited by the lowest contrast, subthreshold stimuli (median, 43.1% increase). Nearly all of the neurons that were modulated by attention ( $36/39 = 92.3\%$ ) had stronger responses to these subthreshold stimuli when they were attended. There is also a clear rightward bias in the histogram across the population as a whole. It is important to note that these increases were observed despite the fact that these stimuli appeared below the neurons' contrast-response thresholds and did not elicit a response above the spontaneous firing rate when they were unattended. Thus, attention reduced contrast-response thresholds across the population. As was observed in the population average responses, the magnitude of changes in firing rate with attention was diminished at higher contrasts.

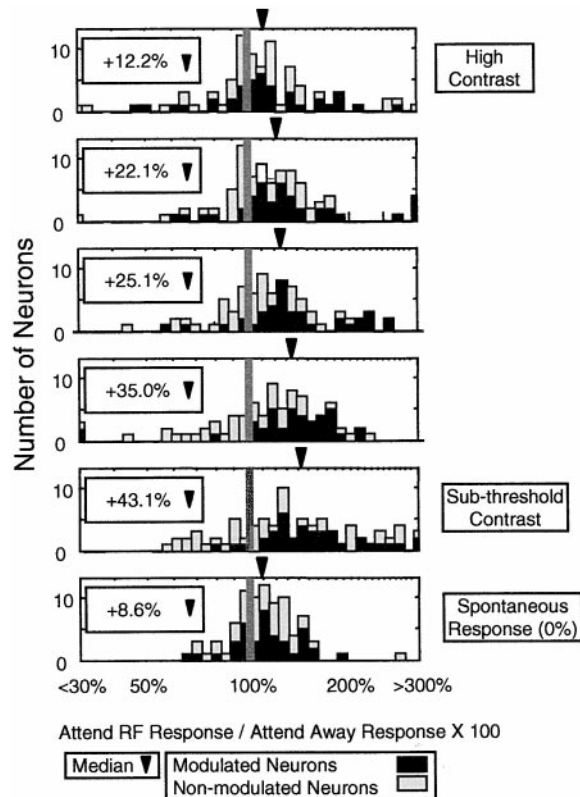
#### Quantifying the Increase in Sensitivity in Contrast Units

The above analyses show that attention increases neuronal sensitivity, resulting in a leftward shift of the contrast-response function. In order to quantify this sensitivity increase in units of contrast, we constructed neurometric functions for each neuron, which estimated how reliably the neuron could detect attended and ignored stimuli as a function of contrast (see Experimental Procedures). Briefly, at each contrast, we computed a receiver operating characteristic (ROC) sensitivity index that reflects how reliably the neuron could detect the stimulus at that contrast. This provided us with five sensitivity measures across contrast for attended stimuli



**Figure 5. Average Effect of Attention as a Function of Contrast**  
 (A) Average neuronal responses to attended and ignored stimuli for neurons that were significantly ( $p < 0.01$ ) modulated by attention, according to a two-way ANOVA of firing rate, with the five contrast levels and attentional state (attend away, attend receptive field) as factors. Thirty-nine out of 84 (46.4%) neurons showed either a significant ( $p < 0.01$ ) main effect of attention or an interaction between attention and contrast.  
 (B) Average neuronal responses for neurons that were not significantly ( $p > 0.01$ ) modulated by attention. In each panel, the gray line shows mean firing rate with attention away from the receptive field during the first 400 ms after stimulus onset. Contrasts increase from 0% (spontaneous firing rate, computed during the 250 ms prior to stimulus onset) on the left to saturation contrast on the right. Solid gray and black lines show mean firing rates elicited by ignored and attended stimuli, respectively. Firing rates are indicated on the left axis. The dashed line shows the percentage change in absolute response with attention (i.e., without subtracting away baseline response), with values indicated on the right axis. The dotted line shows the arithmetic difference in firing rate. Statistically significant differences are indicated by asterisks ( $p < 0.05$ ) and double asterisks ( $p < 0.001$ ). Error bars indicate  $\pm$  two times the standard error of the mean difference in response to attended and ignored stimuli. For neurons that were modulated by attention (A), attention to the receptive field location caused a small but significant increase in spontaneous activity. Attention caused larger and more significant increases in response for intermediate-contrast stimuli. There was a small increase in response with attention to the highest contrast stimulus tested, but this was not statistically significant. As expected, there was little or no effect of attention across neurons that were not individually modulated by attention, according to the ANOVA (B).

and five more sensitivity measures for ignored stimuli. We used a maximum likelihood method (Quick, 1974) to fit each of these sets of five sensitivity measures with a Weibull function (see Experimental Procedures). This is illustrated in Figure 7A, which shows the



**Figure 6. Effect of Attention across Individual Neurons**  
 Each panel shows the distribution of changes in average firing rate across the population, at a given level of contrast. Panels are arranged from saturation contrast (top panel) down to 0% contrast (spontaneous response, bottom panel). The horizontal axis of each panel shows the magnitude of the response to the attended stimulus, stated as a percentage of the response that was elicited by the same stimulus when unattended (without subtracting the baseline response). The gray vertical line indicates attended responses that were equal in magnitude to unattended responses (i.e., no effect of attention). Points to the right of the gray line correspond to response enhancement with attention. Dark bars correspond to the 39 neurons that were statistically significantly modulated by attention, as described in the text, and light bars (which are stacked on top of the black bars) correspond to the 45 neurons that were not significantly modulated by attention. Black arrows along the top of each panel indicate the median attention effect, computed across neurons that were significantly affected by attention. The largest percent increases in response with attention were observed for stimuli that were just below the contrast-response threshold and did not elicit a response when unattended (second panel from bottom). For these subthreshold stimuli, the majority of points are to the right of 100%, indicating an increase in firing rate with attention. Note that elevations in spontaneous activity (bottom panel) were smaller than those observed with subthreshold stimuli, despite the fact that these stimuli did not elicit responses when unattended. Attention effects also diminish in magnitude at higher contrasts (upper panels). Bins are  $0.067 \log_2$  units in width. Average responses were computed over the 400 ms following stimulus onset. Average spontaneous activity was computed over the 250 ms prior to stimulus onset.

Weibull function fits for a single neuron. The neuronal response elicited by the unattended stimulus at 4% contrast could not be differentiated from the neuron's spontaneous firing rate, as indicated by an ROC value of  $\sim 0.5$  (leftmost gray square). The neuron's ability to detect the stimulus steadily increased with contrast

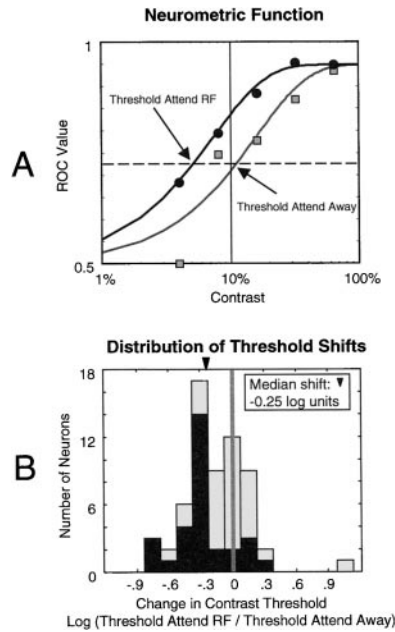


Figure 7. Quantifying Attention in Units of Contrast

(A) Gray squares indicate the ROC sensitivity values (vertical axis) for a single neuron, for nontarget stimuli presented at 4%, 8%, 16%, 32%, and 64% contrast (horizontal axis) while attention was directed away from the receptive field. Black circles indicate corresponding ROC values when attention was directed to stimuli appearing within the receptive field. The gray and black lines indicate the maximum likelihood Weibull function fits to the ROC values with attention directed away from or to the receptive field, respectively. The horizontal dashed line is halfway between the lower asymptote (0.5) and the upper asymptote, which was set equal to the largest ROC value observed for the highest contrast stimulus, in either attention condition. For each Weibull function, we computed the contrast at which the function crossed this threshold.

(B) The distribution of shifts in the Weibull function with attention, across neurons. The horizontal axis shows the magnitude of the shift in the Weibull function with attention. Points to the left of the gray line correspond to neurons for which attention caused a leftward shift in the Weibull function, reflecting an increase in the neuron's contrast sensitivity. Points to the right reflect a rightward shift in the Weibull function. Dark bars correspond to the 30 neurons that were statistically significantly modulated by attention and could reliably be fit with a Weibull function in both attention conditions. Light bars (which are stacked on top of the black bars) correspond to the 31 neurons that were not significantly modulated by attention and could be fit in both conditions. The black arrow along the top of the panel indicates the median shift with attention, computed across neurons that were significantly affected by attention ( $-0.25$  log units, equivalent to a 79% increase in contrast). Across the population, the median shift was  $-0.18$  log units (equivalent to a 51% increase in contrast). Mean shifts were  $-0.27$  log units across neurons that were significantly affected by attention and  $-0.15$  log units across the population.

(gray squares). When attention was directed toward the stimulus in the receptive field, ROC values were higher and reached an asymptote of 0.95 at the highest contrast tested. We quantified the shift in the best-fit Weibull function for each neuron by comparing the contrast at which each curve reached half its maximum height. The example neuron reached this threshold at 11.1% contrast for unattended stimuli and 5.1% contrast for attended stimuli, a reduction of 0.34 log units. Thus, this

neuron's ability to detect a stimulus could be equivalently improved by either directing attention to the stimulus or increasing its contrast by slightly more than a factor of two.

Across the population of neurons, attention shifted the Weibull function to the left, reflecting increased sensitivity. This is illustrated in Figure 7B, which shows the distribution of shifts across the 61 neurons that could reliably be fit by Weibull functions in both attention conditions. For neurons that were significantly modulated by attention (black bars), the median shift was  $-0.25$  log units of contrast, which is equivalent to a 79% increase in the effective contrast of attended stimuli. This estimate is consistent with the increase in response observed across the population, computed for neurons that were modulated by attention (see Figure 5A). Across the entire population (black bars + gray bars), the median shift was  $-0.18$  log units of contrast, or a 51% increase in effective contrast with attention.

### Attention Effects with Preferred Stimuli

Diminished effects of attention at high contrast could potentially be due to our use of nonoptimal stimuli. For example, at high contrast, nonoptimal stimuli might activate off-orientation suppression, which could potentially counteract further increases in response with attention. To rule this out, we recorded the responses of 26 additional neurons using nontarget stimuli that were of the preferred orientation and spatial frequency for each neuron. Stimuli ranged from just above the contrast-response threshold up to saturation contrast. The change in the average response above baseline was +73%, +21%, +3%,  $-7\%$ , and  $-2\%$  at each of the successively higher contrasts. We performed a paired t test across all 26 neurons at each level of contrast to assess the statistical significance of changes in firing rate with attention. Attention had a significant effect at the lowest four contrasts ( $p = 0.01$ ,  $p = 0.02$ ,  $p = 0.02$ ,  $p = 0.04$ ) and no significant effect at the highest contrast tested ( $p = 0.58$ ). Thus, the reduction in attentional effects at high contrast does not appear to be due to the use of nonoptimal stimuli.

### Discussion

The results support the hypothesis that attention causes an increase in V4 neurons' sensitivity but without a substantial increase in the response to high-contrast stimuli. This increase in sensitivity is reflected in a leftward shift in the contrast-response function. Neurons responded to attended stimuli that were too faint to elicit a response when unattended (a reduction in contrast-response threshold). The largest changes in firing rate with attention were observed for stimuli that were within the dynamic range of the contrast-response function. The effect of attention diminished at high contrasts, reaching a minimum for stimuli that were above the saturation point on the neuron's contrast-response function. This reduction in the magnitude of attention effects at high stimulus contrast was not a ceiling effect resulting from neurons being driven to their highest possible firing rates, as the stimuli used were of suboptimal orientation and spatial frequency and did not drive neurons to their

highest possible firing rates. The median increase in neuronal sensitivity with attention was equivalent to increasing the physical contrast of the stimulus by 51%.

#### Timing of Attention Effects

As stimulus contrast is increased, neuronal response latencies become shorter in primary visual cortex and, presumably, in subsequent visual areas (Gawne et al., 1996). Indeed, we observed shorter response latencies at high contrast in V4, for both attended and unattended stimuli. However, the increase in average firing rates with attention that we observed for low-contrast stimuli was not accompanied by any obvious decrease in response latency. Thus, the increase in effective stimulus contrast with attention in V4 is not identical to an increase in physical stimulus contrast. What mechanism might then account for the increased contrast sensitivity with attention? One possibility is that attention may increase the efficacy of inputs from afferent neurons to the recorded neuron. The effect on the target neuron would be similar to an increase in the strength of the presynaptic signal itself. Because this increase in strength of inputs with attention would occur downstream from the V1 (or earlier) mechanisms that cause latencies to decrease with physical contrast, the attentional effects on responses would not be accompanied by latency changes in V4.

We have previously proposed a model for the changes in firing rate that occur when attention is directed to one of two stimuli that appear simultaneously within the receptive field (Reynolds et al., 1999), and this model predicts the present results with a single stimulus in the receptive field as well. According to this model, when a single stimulus appears, this activates afferent neurons that send both excitatory and (through inhibitory interneurons) inhibitory input to the recorded cell. As the strength of afferent inputs increases, the neuron approaches a maximum firing rate for that stimulus, which is determined by the ratio of excitatory to inhibitory input. Consistent with the finding that V4 neuron responses are a sigmoidal function of the logarithm of contrast, the model predicts that firing rate should be a sigmoidal function of the logarithm of input strength. When attention is directed to the stimulus, the resulting increase in effective stimulus strength increases the strength of excitatory and inhibitory input to the recorded neuron, resulting in a leftward shift of the sigmoidal function.

Consistent with the present data, the model predicts no changes in response onset latency with attention, and it offers a potential explanation of the finding that the effects of attention on the response to low-contrast stimuli occurred earlier after stimulus onset (~100 ms after stimulus onset) than the attention effects on high-contrast stimuli (~200 ms after stimulus onset). According to the model, the effects of attention should be smallest when afferent inputs are strongest. Such strong inputs presumably occur during the initial transient response to a high-contrast stimulus, where firing rates are maximal. This might delay any effects of attention until later in the response, when afferent inputs are weaker. For low-contrast stimuli, afferent inputs are weak and there is often not a pronounced response

transient, thereby allowing the attention effects to be expressed at an earlier phase of the response.

#### Task Difficulty

An alternative explanation for the greater effects of attention with low contrast stimuli is that such stimuli are harder for the animal to detect, i.e., they demanded a greater degree of attentional effort. Indeed, earlier experiments have shown that the magnitude of attention effects in V4 increases with task difficulty (Spitzer et al., 1988). It is unlikely, however, that the present effects are due to a change in task difficulty with target contrast, because on each trial the contrast of each stimulus in the sequence was randomized. The monkeys could not predict the contrast of the target until it appeared at the end of the trial. Therefore, they could not adjust their attentional effort to compensate for target contrast until after the disappearance of the nontarget stimuli. Furthermore, because the contrasts of the nontargets were randomized, a high-contrast nontarget was just as likely to appear in a trial with a high-contrast target as it was to appear in a trial with a low-contrast target.

The possibility remains, however, that the monkeys analyzed the contrast of each successive stimulus "on the fly" and then withdrew attention from high-contrast stimuli, so as to expend a lower level of effort determining whether the high-contrast stimulus was a target or a nontarget. This would require the monkey to immediately reallocate attention to the cued location in order to determine the contrast of the succeeding stimulus. Moreover, the duration of the blank interval between successive stimuli varied randomly. In order to attend reliably to the next stimulus in the sequence, the monkey would need to redeploy attention to the cued location within 400 ms of the offset of the current stimulus, which was the shortest interstimulus interval used. The target could appear after as many as five nontargets, so this strategy would require the monkey to rapidly reallocate attention up to ten times within a trial before detecting the target. It would seem that such a strategy would increase, rather than reduce, the effort expended by the monkey.

The most direct evidence that the monkeys did not pursue this strategy comes from the timing of attentional modulation. If monkeys initially attended to the cued location and only withdrew attention after determining that the stimulus was of high contrast, then the effects of attention should be most evident at the onset of the response and should then diminish after attention was withdrawn from a high-contrast stimulus. In fact, the timing of the attention effect was exactly the opposite. It was completely absent during the initial response, emerging weakly only later in the response (see Figure 4).

A related possibility is that after determining that a stimulus is of low contrast, monkeys allocate additional attentional effort. This explanation would predict that for low-contrast stimuli, attentional effects on the response should be observed only after the monkey hypothetically determined the contrast of the stimulus and increased its attentional effort. However, again, we find the opposite pattern of results. The effects of attention typically began at the initial onset of the response that was evoked by low-contrast stimuli (see Figure 4).



### High-Contrast Stimuli Attracting Attention

Another possible explanation for diminished effects with high-contrast stimuli is that such stimuli may have attracted the monkey's attention. As a result, even when the monkey was instructed to attend outside the receptive field, the appearance of a high-contrast stimulus in the receptive field could attract the monkey's attention to the receptive field location. Hence, any difference in firing rate due to the original attention instruction would be eliminated shortly after the appearance of the high-contrast stimulus in the receptive field. In fact, we find the opposite pattern of results. The increased firing with attention was absent at the very beginning of the response to higher contrast stimuli and only emerged later in the response when, according to the above explanation, it should have disappeared. Therefore, it is unlikely that the diminished effects with high-contrast stimuli are due to the monkey inadvertently attending to the un-cued high-contrast stimulus in the receptive field.

### Attention and Visual Saliency outside V4

The relationship between visual saliency and attention has recently been investigated in the superior temporal sulcus and the lateral inferior parietal cortex (area LIP) of the macaque. Consistent with the present results, a preliminary report from Treue and Martinez Trujillo (1999, Soc. Neurosci., abstract) indicates that, as in V4, attention effects in the superior temporal sulcus diminish at high contrast. This suggests that a common attentional mechanism may be at work in both the dorsal and ventral processing streams. One possibility is that posterior parietal cortex modulates neuronal sensitivity with attention in both processing streams. It has anatomical connections with some areas in both streams, including area V4, and Gottlieb et al. (1998) have found that neurons in area LIP of parietal cortex increase responses to potentially relevant stimuli. Furthermore, patients with parietal lesions are often impaired in attention-demanding tasks (see, e.g., Friedman-Hill et al., 1995).

### Relationship to the Effect of Attention with Multiple Stimuli in the Receptive Field

Prior spatial attention studies using multiple high-contrast stimuli within the receptive field of V4 neurons have consistently shown large changes in firing rate with attention (Moran and Desimone, 1985; Luck et al., 1997; Reynolds et al., 1999). By comparison, the effects of attending to a single stimulus (of high or unspecified contrast) within the receptive field has ranged from negligible to modest in a variety of studies (Moran and Desimone, 1985; Haenny et al., 1988; Spitzer et al., 1988; Maunsell et al., 1991; Motter, 1993; Connor et al., 1996, 1997; Luck et al., 1997; McAdams and Maunsell, 1999a, 1999b). In addition to differences in the magnitude of attentional effects with single and multiple stimuli, there are also qualitative differences in the effects of attention. With a single stimulus, the effect of attending to it is, if anything, an increase in firing rate, whereas with two stimuli competing within the receptive field, attention may have opposite effects on responses depending on the neuron's selectivity. If a good and a poor stimulus are placed within the receptive field, and if attention is directed to the good stimulus, the response to the pair

will *increase* to a level comparable to the response elicited by the good stimulus alone. However, if attention is directed to a poor stimulus in the receptive field, this typically *reduces* the response to the pair, so that it approaches the response elicited by the poor stimulus alone (Reynolds et al., 1999). The differences between the single and multiple stimulus configurations cannot be explained by a simple increase in response gain with attention, but rather fit within the framework of a biased competition model of attention (Desimone and Duncan, 1995; Reynolds et al., 1999).

### Variability across Studies

The present results show that the duration and luminance contrast of stimuli help determine whether or not attention influences neuronal firing rates, and it was previously shown that attention effects vary with task difficulty (Spitzer et al., 1988). Variation in these factors across studies may explain why some previous studies of attention have found increases in responses with a single stimulus in the visual field (Spitzer et al., 1988; Connor et al., 1996, 1997; McAdams and Maunsell, 1999a, 1999b), while others have not (Moran and Desimone, 1985; Haenny et al., 1988; Maunsell et al., 1991; Motter, 1993; Luck et al., 1997). For example, Luck et al. (1996) failed to find attention effects when a single stimulus appeared within the receptive field, whereas McAdams and Maunsell did find such effects, and both studies used demanding tasks. However, the stimulus appeared for only 50 ms in the study of Luck et al., compared to 500 ms in the McAdams and Maunsell study, and we have found in the present study that attentional effects are not present for the first 100 ms of the response at high contrast. Furthermore, although Luck et al. used a flashed high-contrast stimulus with sharp edges, McAdams and Maunsell used a smooth Gabor stimulus that was low contrast for part of the stimulation cycle. Thus, differences in stimulation time or contrast could easily account for the differences in results.

### Features versus Intensity

The study of McAdams and Maunsell (1999a), coupled with the present results, point to a fundamental distinction between the neural circuitry underlying the processing of stimulus features, such as orientation, and the processing of stimulus *intensity*, such as luminance contrast, a distinction that has also been made in studies of primary visual cortical neurons (Dean, 1981; Tolhurst et al., 1981; Albrecht and Hamilton, 1982; Sclar and Freeman, 1982; Skottun et al., 1987). McAdams and Maunsell measured the effect of attention on the responses of V4 neurons to luminance gratings presented across a range of orientations. They found that attending to the stimulus increased neuronal responses (above baseline) to preferred and poor stimuli by a constant percentage (on average, 26%), resulting in the *largest* increases in firing rate for preferred orientation stimuli that elicited the strongest responses when unattended. In contrast, in the present experiment we found that the increase in response with attention varied as a function of contrast, and the *smallest* changes in response with attention were observed at high contrast, where the response to the unattended stimulus was strongest. The

two results are compatible if one assumes that an increase in contrast sensitivity (such as we observed) causes an equivalent percentage increase in response across orientations, at fixed contrast (such as what McAdams and Maunsell observed). This assumption seems reasonable based on studies that have found a gain multiplication of orientation tuning with increases in the physical contrast of the stimulus (Dean, 1981; Sclar and Freeman, 1982).

### Changes in Sensitivity with Attention in Humans

Event-related potential (ERP) studies have found that attention increases the magnitude of voltage deflections recorded at scalp sites overlying lateral prestriate visual cortex, which may reflect an increase in the strength of neuronal signals generated by attended stimuli in humans (reviewed by Mangun, 1995; Hillyard and Anllo-Vento, 1998; Mangun et al., 1998). Psychophysical studies have provided evidence that human observers are more sensitive to stimuli appearing at an attended location (see, e.g., Bashinski and Bacharach, 1980; Posner et al., 1980; Downing, 1988; Hawkins et al., 1990; Reinitz, 1990; Muller and Humphreys, 1991; Luck et al., 1994; Lee et al., 1997). Recently, Blaser et al. (1999), using an ambiguous motion stimulus paradigm, have demonstrated that attention to a stimulus increases its effective salience. In the present experiment, we have identified possible neural correlates of these electrophysiological and behavioral effects of attention in humans.

Perhaps the most directly comparable psychophysical study is the recent experiment of Lu and Dosher (1998), who measured changes in luminance contrast thresholds as a function of spatial attention. Subjects simultaneously discriminated the orientation of Gabor patterns appearing at two locations to the right and left of fixation. When subjects were cued to attend preferentially to one of the two locations, the contrast threshold at that location decreased by 17%. Although the magnitude of this reduction in threshold is smaller than the improvement in contrast thresholds observed in the present study, the similarity of the effects of attention on contrast thresholds observed at the neuronal and the behavioral levels lends support to the idea that behavioral improvements in performance with attention may be the result of improvements in sensitivity among individual neurons.

### Experimental Procedures

#### Subjects and Surgical Techniques

The two adult male rhesus monkeys used in this experiment were cared for according to National Institutes of Health guidelines for the care and use of animals. Many of the details of the surgical techniques have been described previously (Miller et al., 1993). Briefly, two adult male rhesus monkeys (*Macaca mulatta*) were surgically implanted with a headpost, a scleral eye coil, and a recording chamber. Surgery was conducted under aseptic conditions with isoflurane anesthesia, and antibiotics and analgesics were administered postoperatively. Preoperative magnetic resonance imaging (MRI) was used to identify the stereotaxic coordinates of V4. V4 recording chambers were placed over the prelunate gyrus. The skull remained intact during the initial surgery, and small holes (~3 mm in diameter) were later drilled within the recording chambers under ketamine anesthesia and xylazine analgesic to expose the dura for electrode penetrations.

#### Confirmation of Recording Sites

At the beginning of the study, several penetrations were made in each chamber to ensure that the electrode was in the appropriate visual area. This was determined by assessing receptive field sizes, topographic organization, and feature preferences at each site. All implants were nonferromagnetic (plastic recording chambers, titanium screws, brass headposts). After our experimental data were collected, we verified the locations of our recording sites using additional MRI scans (data not shown). We rescanned both monkeys with a marker electrode (sharpened tungsten microelectrode) inserted in each recording chamber at coordinates used during recording. We used a plastic cylinder that fit snugly inside the recording well to hold the marker electrode in place during the scan. At each end of the cylinder was a grid that was perforated with small holes, spaced 1 mm apart (Christ Instruments, Damascus, MD). Each marker electrode was lowered through the grids and into the brain to a depth of ~2 cm beneath the dura using the same micropositioner and x-y stage that had been used during recording. Before removing the micropositioner and x-y stage, a drop of glue was applied to hold the marker electrode in the grid. After removing the micropositioner and x-y stage, the end of the electrode that was protruding from the recording well was then cut, and a plastic cap was placed over the recording chamber during the scan. These marker electrodes were clearly visible in each scan. The positions of these markers, the positions of electrode tracks made during recording, and the positions of the holes in the skull beneath each recording chamber all verified that our recording sites were appropriately located in area V4 on the prelunate gyrus.

#### Recording Technique

Recordings were obtained from a tungsten microelectrode, and waveforms from individual neurons were isolated using a standard online spike-sorting system (Signal Processing Systems, Australia). In most cases, two neurons could be recorded simultaneously and differentiated on the basis of the size and shape of the spike waveform. We made no effort to select neurons from a particular layer of cortex. Instead, we recorded from the first neurons encountered that could be clearly isolated.

#### Stimuli

All stimuli were 250 ms in duration. Nontarget stimuli were rectangular patches of sinusoidal luminance grating, typically about 0.4° wide by about 1.5–2° in length. Targets were square patches of grating that were typically 1.5° in length and width, rotated to be 45° from the orientation of the nontargets and of the same spatial frequency as the nontargets. We selected the orientation and spatial frequency of nontargets from a standard set of four orientations (vertical, 45°, horizontal, 135°), with spatial frequencies of 0.5, 1, 2, 4, or 8 cycles/°. It was important to be sure that the effect of attention on firing rate would not be reduced at high contrast simply because high-contrast stimuli drove neurons to their maximum physiological firing rate. Therefore, for stimulus-selective neurons, we chose stimuli that were not of the optimal orientation or spatial frequency for the neuron. At the beginning of each recording session, we recorded the responses to the 20 possible combinations of orientation and spatial frequency, presented at 40% luminance contrast, while the monkey passively fixated a fixation point at the center of the computer screen. The preferred stimulus was taken to be the stimulus (from our set of four orientations and five spatial frequencies) that elicited the highest firing rate during this initial mapping. We selected the nontarget stimulus to be a stimulus that elicited a clear response (averaged over the 400 ms following stimulus onset) that was smaller than the response elicited by the preferred stimulus. For nonselective cells, the orientation and spatial frequencies of the nontarget stimuli were chosen randomly. To quantify the difference in response to preferred and nonpreferred stimuli, we recorded responses to preferred stimuli on probe trials, in which the preferred stimulus appeared instead of the usual nontarget stimulus while the monkey performed the attention task at the position that was opposite the receptive field. For a few cells, we also measured attentional modulation using nontarget stimuli that were of the neurons' preferred orientation and spatial frequency.

After selecting the spatial frequency and orientation of the target and nontarget stimuli, we determined the dynamic range of each

neuron's response as a function of stimulus contrast (%contrast = maximum luminance - minimum luminance)/(maximum luminance + minimum luminance) × 100). These measurements were performed during passive fixation by presenting the nontarget stimulus across a range of seven contrasts (1.25%, 2.5%, 5%, 10%, 20%, 40%, 80%). Responses to this stimulus provided an initial estimate of the *contrast threshold* of the cell, its *dynamic range*, and the point of *contrast saturation*. Based on these estimates, we selected five contrasts that spanned the neuron's dynamic range and were spaced at equal log intervals of contrast (typically doubling the next lower contrast). The highest contrast stimulus was selected to be at or above the point where further increases in contrast did not result in further increases in firing rate. Note that the highest contrast stimulus often elicited responses that were greater than the second highest contrast stimulus, which was selected to be within the dynamic range of the contrast-response function.

### Task

Monkeys fixated a small (0.1° × 0.1°) spot at the center of a computer screen throughout each trial. Fixation was measured using a scleral eye coil, and trials were terminated if eye position deviated from fixation by 0.6° or more. For the neuronal data reported here, stimuli appeared at two locations: one at the center of the receptive field of the neuron being recorded and the other at a position of equal eccentricity across the vertical meridian from the receptive field. At the beginning of a block of trials, several instruction trials were presented in which a white box appeared at one of the two possible stimulus locations (see Figure 2A). The box cued the monkey to attend to that location. Sequences of stimuli appeared at both locations. Most stimuli were rectangular nontargets, but occasionally, a rotated square target would appear at the cued location. The monkey received a juice reward if it released a bar within a time window of 200–500 ms after target onset. If the monkey released the bar outside of this 300 ms time window, or failed to release the bar when the cued target appeared, the computer screen went blank, and after a brief delay a new sequence began. On 20% of trials, a distractor "foil" target appeared at the noncued location, and the monkey was not rewarded if it responded to the foil.

Once the monkey was responding reliably to targets appearing at the cued location, and was ignoring distractor targets at the uncued location, the cue was removed and the monkey had to continue to perform the task in the absence of the cue (see Figure 2B). We carefully monitored behavioral performance to ensure that monkeys continued to respond to targets at the location that had been cued, and to ignore distractor targets at the other location. Occasionally, monkeys responded to several distractor targets in a row, indicating that they had misunderstood the cue. When this occurred, we immediately terminated the block of trials and recued the monkey to attend to the correct location.

The period of time between successive stimulus onsets (stimulus onset asynchrony [SOA]) varied across a uniform distribution from 650–800 ms. While SOAs varied randomly for each stimulus, onset times were matched at the two locations, so stimuli at the two locations appeared synchronously. On each trial, one to six stimuli appeared (at each location). The number of stimuli appearing on a given trial was selected at random from a uniform distribution. Therefore, the monkey could not know in advance when the target would appear and had to attend to the cued location throughout the trial in order to detect the target, release the bar, and earn the reward.

Because the contrast of each stimulus was chosen at random from the set of five possible contrasts, the monkeys did not know in advance whether the target that would appear at the end of a trial would be of high contrast or low contrast. Thus, differences in the magnitude of attention effects for nontarget stimuli could not reflect variation in attentional effort with target contrast.

### Analysis of Neuronal Responses

Responses were analyzed only for correctly performed trials, excluding instruction trials. All data analysis was restricted to nontarget stimuli because neuronal responses to target stimuli were typically interrupted by the behavioral response or the delivery of reward, which only occurred (on correct trials) after the appearance

of the target. In addition, the larger number of nontarget stimuli provided a more reliable measure of response strength.

Because the contrasts of targets and nontargets were selected separately, the lower performance with the lowest contrast target stimuli did not affect the number of trials recorded for low-contrast nontarget stimuli. On average, for each neuron, 19.7 stimulus repetitions at each contrast level were presented with attention away from the receptive field, and 21.1 stimulus repetitions were presented at each contrast level with attention to the receptive field. The average number of stimulus repetitions in each attention condition was 22.7 at the lowest contrast tested and 25.2, 16.2, 18.9, and 19.3 repetitions at each successively higher contrast.

To analyze the time course of changes in firing rate with attention, we divided the period of time following stimulus onset into 100 ms windows, and performed paired t tests on average firing rates across neurons with and without attention directed to the receptive field (see Figure 4). To separately analyze neurons modulated by attention (see Figures 5 and 6), we performed, for each neuron, a two-way analysis of variance (ANOVA) of firing rate during the 400 ms following stimulus onset. This period was chosen because it included the full response at all contrasts tested (see Figure 4). Neurons were classified as being modulated by attention if they showed either a significant ( $p < 0.01$ ) main effect of attention or an interaction between attention and contrast.

To quantify the increase in sensitivity with attention (see Figure 7), we computed neurometric functions for each neuron, using a modification of a method used by Britten et al. (1992) to quantify the sensitivity of MT neurons to motion stimuli. For each neuron, we computed two neurometric functions: (1) one for responses recorded when attention was directed to the stimuli appearing within the receptive field, and (2) a second for responses recorded when attention was directed away from the receptive field. This was done in two steps. First, for each contrast, we computed a detection index indicating how reliably the neuron's stimulus-evoked responses could be discriminated from its spontaneous activity (i.e., how reliably the neuron could detect the presence of the stimulus). Second, we separately fit a Weibull function to each set of five sensitivity measures (attend away, attend receptive field). The detection index measured the degree of overlap between the distribution of trial-by-trial stimulus-evoked responses and the trial-by-trial distribution of spontaneous activity. Stimulus-evoked responses were computed by averaging the spike rate during the 400 ms following stimulus onset. Spontaneous activity was computed by averaging the spike rate during the 250 ms period prior to stimulus onset.

The detection index was the area under a receiver-operator-characteristic (ROC) curve, which was constructed by plotting the probability of correctly detecting the presence of the stimulus (the probability of "hits") as a function of the probability of misclassifying spontaneous activity as a stimulus-evoked response (the probability of "false alarms"), across all possible decision thresholds. The area under the ROC curve provided a nonparametric measure of the performance of a hypothetical ideal observer judging whether or not a stimulus was present by monitoring the responses of the neuron. A value of 0.5 indicates that the stimulus-evoked response could not be discriminated from the spontaneous activity of the neuron. Higher values indicate better detection, with a maximum possible value of 1.0 indicating that the neuronal response was so reliably different from the spontaneous activity that the neuron could signal the presence of the stimulus every trial. The computation of ROC curves is further described in McNicol (1972).

We computed this index for each stimulus contrast, with and without attention. To quantify the effect of attention as a function of contrast, we fit separate functions to the five ROC detection indices measured with and without attention to the receptive field stimulus (see Figure 7A). We used a maximum-likelihood method (Quick, 1974) to fit these data using a Weibull function, which is of the form

$$y = f(x) = 1 + (u - 1) \left( 1 - 2^{-\frac{x^\beta}{c^\beta}} \right)$$

where  $x$  is the luminance contrast and  $y$  is the fit to the ROC curve areas. We set the lower asymptote,  $1$ , to 0.5 because, logically, a neuron cannot detect a stimulus of zero contrast. The upper asymptote,  $u$ , was set equal to the higher of the two ROC values measured

at saturation contrast in the two attention conditions. The free parameter,  $\beta$ , determines the slope of the function. The offset parameter,  $\alpha$ , is the contrast at which the Weibull function reaches the halfway point between its lower asymptote,  $l$ , and its upper asymptote,  $u$ . In computing maximum likelihood Weibull fits, we assumed that the performance of the hypothetical ideal observer could be modeled as a binomial process, with the probability of correctly detecting the stimulus at a given contrast being equal to the ROC area computed at that contrast. The value of the binomial distribution parameter,  $N$ , at each contrast and in each attention condition was equal to the number of stimulus repetitions.

For each neuron, we quantified the shift in the Weibull function with attention by computing the ratio between the value of  $\alpha$  when the monkey attended to the receptive field location and the value of  $\alpha$  when the monkey attended away. Ratios less than 1 correspond to neurons for which attention shifted the Weibull function to the left (an increase in contrast sensitivity). In order to state this shift in log units of contrast, we computed the logarithm of the ratio between these two values (see Figure 7B).

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