Effects of Spatial Attention on Contrast Response Functions in Macaque Area V4

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Williford, Tori and John H. R. Maunsell. Effects of spatial attention on contrast response functions in macaque area V4. *J Neurophysiol* 96: 40–54, 2006; doi:10.1152/jn.01207.2005. Previous single-unit studies of visual cortex have reported that spatial attention modulates responses to different orientations and directions proportionally, such that it does not change the width of tuning functions for these properties. Other studies have suggested that spatial attention causes a leftward shift in contrast response functions, such that its effects on responses to stimuli of different contrasts are not proportional. We have further explored the effects of attention on stimulus-response functions by measuring the responses of 131 individual V4 neurons in two monkeys while they did a task that controlled their spatial attention. Each neuron was tested with a set of stimuli that spanned complete ranges of orientation and contrast during different states of attention. Consistent with earlier reports, attention scaled responses to preferred and nonpreferred orientations proportionally. However, we did not find compelling evidence that the effects were best described by a leftward shift of the contrast response function. The modulation of neuronal responses by attention was well described by either a leftward shift or proportional scaling of the contrast response function. Consideration of differences in experimental design and analysis that may have contributed to this discrepancy suggests that it was premature to exclude a proportional scaling of responses to different contrasts by attention in favor of a leftward shift of contrast response functions. The current results reopen the possibility that the effects of attention on stimulus-response functions are well described by a single proportional increase in a neuron's response to all stimuli.

INTRODUCTION

Although many studies have demonstrated that attention modulates activity in a range of cortical visual areas, relatively few have examined how attention affects neuronal stimulus-response functions. Two experiments examined how attention affects orientation tuning curves in V4 (McAdams and Maunsell 1999a) and direction tuning curves in the middle temporal area (MT) (Treue and Martinez-Trujillo 1999). Both found that the effects of attention could be described as a vertical scaling of tuning curves with no change in the width of the tuning curve. In the case of V4 orientation tuning, the change was described as a fixed scaling of firing rate above spontaneous activity (multiplicative scaling of the driven rate) as if attention increased the gain of the response above background (response gain, Fig. 1, *A* and *D*). In the case of MT direction tuning, it was not clear whether attention increased the gain of the response or the gain of the overall activity of the neurons (activity gain, Fig. 1*E*).

More recently, other studies have examined how attention affects contrast response functions in V4 (Reynolds et al. 2000)

and MT (Martinez-Trujillo and Treue 2002). Both studies reported an effect that differed from the response or activity gain seen for orientation and direction. Instead they found that attention increased the effective contrast of each attended stimulus (Fig. 1*C*), resulting in a leftward shift of the contrast response function. This effect has been called contrast gain. The horizontal shifts of contrast gain are similar to the changes in the sensitivity of individual neurons in monkey visual cortex seen after contrast adaptation (Allison et al. 1993; Carandini et al. 1997; Kohn and Movshon 2003; Sclar et al. 1989).

Although the contrast gain described for contrast response functions differs from the response or activity gain seen for orientation and direction tuning, the effects are not inconsistent. Both could be explained by a mechanism that effectively adds contrast to attended stimuli. The measurements of orientation and direction tuning used stimuli of a single contrast. Attention could affect responses to stimuli of all orientations or directions proportionally if they have the same contrast, but the proportion by which they are scaled may vary depending on stimulus contrast as shown in Fig. 1*B*. In this hypothetical case, orientation or direction tuning curves for low- or high-contrast stimuli are each scaled proportionally by attention (activity gain), but the strength of the attentional modulation varies with contrast (contrast gain).

We were interested in further studying the effects of attention on different contrasts for several reasons. One was the prospect of learning more about the sites and mechanisms by which attention acts. Collectively, the results described in the preceding text suggest that attention acts by a mechanism that is more complex than a simple change in sensitivity. For example, they imply that a neuron responding with a given firing rate will be only modestly modulated by attention if the response is generated by a high-contrast stimulus of nonpreferred orientation or direction (Fig. 1*B*, b and b′) but much more affected if the same firing rate is generated by a low-contrast stimulus of preferred orientation or direction (Fig. 1*B*, a and a′), although the initial firing rates (a and b) are identical. This complexity in the way attention modulates a given firing rate could provide leverage for insights into where and how it acts.

We were also interested in studying the effects of attention on different contrasts because some earlier observations are difficult to reconcile with contrast gain. Contrast gain implies that there should be no effect of attention on responses that are well into the high or low saturating portions of a contrast response function (Fig. 1*C*). Neurons in MT are sufficiently
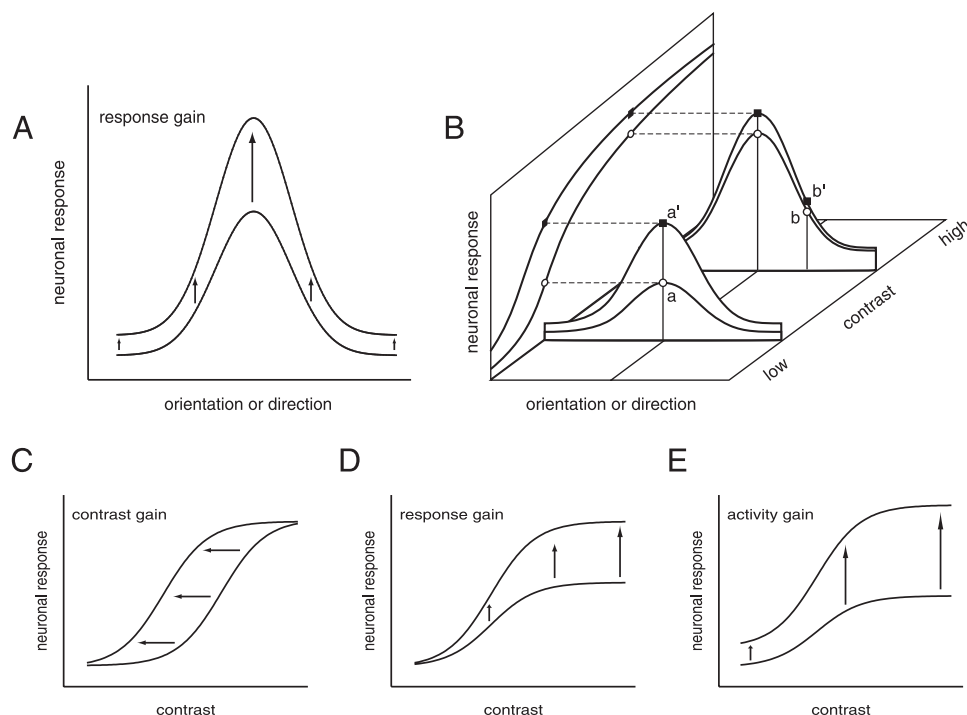

FIG. 1. Descriptive models of the effects of attention on visual responses. See text for discussion. *A*: effect of response gain on an orientation or direction tuning curve. *B*: hypothetical actions of attention on contrast response functions and orientation or direction tuning curves. *C*: effect of contrast gain on a contrast response function. *D*: effect of response gain on a contrast response function. *E*: effect of activity gain on a contrast response function.

sensitive to low contrasts that the response of a typical MT neuron is far into saturation at high contrasts (median response at 99% of the maximum attainable firing rate by 33% contrast) (Sclar et al. 1990; see also Thiele et al. 2000). Nevertheless, most of the effects of attention described in MT have been measured using stimuli with high contrast (Cook and Maunsell 2002, 2004; Recanzone and Wurtz 2000; Seidemann and Newsome 1999; Treue and Maunsell 1996; Wegener et al. 2004). If attention acts by a mechanism like contrast gain, these studies should have seen little or no attentional modulation. Similarly, contrast gain predicts no effect on spontaneous activity, but such effects have been reported (Luck et al. 1997; Reynolds et al. 2000).

We have re-examined how spatial attention affects the responses of V4 neurons to stimuli of different contrasts. Unlike the previous studies, we did not find support for the idea that the effects of attention are best described by contrast gain. Instead we found that although contrast gain (Fig. 1*C*), response gain (Fig. 1*D*), and activity gain (Fig. 1*E*) all provide adequate fits to the data, response gain and activity gain provide marginally superior descriptions. These results reopen the possibility that the mechanisms of attention can be well explained as an increase in sensitivity for all stimuli.

METHODS

Behavioral task

The animal protocols used in this study were approved by the Baylor College of Medicine Institutional Animal Care and Use Committee. Two male monkeys (*Macaca mulatta*, 8 and 9 kg) served as subjects. Each was implanted with a scleral search coil and a head post under general anesthesia. After recovery, the animal was trained to do an orientation-change detection task (Fig. 2). On each trial, the animal maintained fixation (within 1°) on a small central spot (0.1–0.2° diameter) while series of Gabor stimuli were flashed on either side. On each trial, most of the Gabors had the same orientation. The animal's

task was to detect when a Gabor with a different orientation (the target) appeared on the cued side and respond by making a saccade to the target's location within 500 ms of its appearance. The animal received a juice reward for correctly completed trials. The size of the orientation change was adjusted to challenge the animals. We gener-
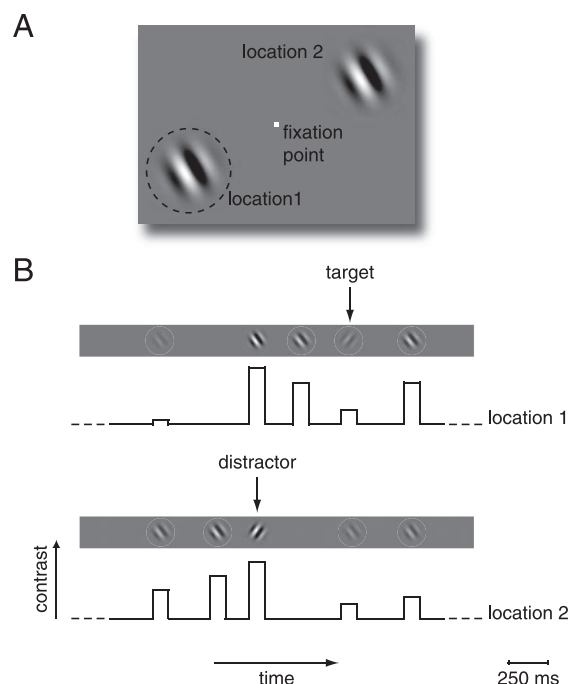

FIG. 2. Schematic of stimulus presentation and timing. *A*: 1 stimulus was positioned to fall on the receptive field of the neuron being recorded (dashed circle). On each trial the animal had to detect orientation changes on the cued side. The animal fixated on the central fixation point while awaiting the change. *B*: each stimulus appeared for 94 ms with a 141- to 294-ms inter-stimulus period. The contrast of each stimulus was randomly selected from a predefined set. The animal was required to respond when the orientation changed on the cued side but not if the orientation changed on the uncued side.

ally kept the animal's performance in the range of 50–65% correct (excluding breaks in fixation). Because the Gabors were small, brief and eccentric (see following text) orientation differences were typically ≥70°.

Instruction trials were used to cue the animal to attend only to stimuli on one side. On these trials, a series of Gabors appeared on one side only, and the animal was trained to continue responding to this side in subsequent trials after the second series was reintroduced. The target side changed after 16 trials had been successfully completed on one side. Two instruction trials were inserted whenever the animal needed to attend to a different side. Although most of the stimuli on the uncued side had the same orientation as those on the cued side, occasionally stimuli with different orientations were inserted as distractors. If the animal responded to these orientation changes on the uncued side, the trial ended without reward.

Visual stimuli

The visual stimuli were achromatic Gabors presented on a calibrated video display (1,024 × 768 pixels, 28 × 38°, 85-Hz frame rate) placed 57 cm in front of the animal. The Gabors were odd-symmetric so that they introduced no overall change in luminance. Each appeared for 94 ms, and each interstimulus period was randomly selected from the range of 141–294 ms. The timing of stimuli on both sides of fixation was synchronized. The target appeared at a time that was randomly selected from an exponential distribution that was truncated at 5 s (flat hazard function for orientation changes) with the restriction that the target could never be the first stimulus in the series. About 10% of trials reached 5 s without a change in Gabor orientation at which time the trial ended, and the animal was rewarded without responding.

A single orientation was used on each trial, selected at random from two or four evenly spaced orientations. Although the orientation was fixed on each trial, the contrast of each Gabor was selected randomly from a range of 5–11 values. By varying the contrast within trials and the orientation between trials, we measured neuronal responses to all combinations of orientations and contrasts. The set of contrasts used was fixed during recording from each neuron. The range of contrasts always included 0%, with the remaining contrasts starting at 100% and decreasing in steps of a fixed proportion to a minimum of about 2%. The 0% condition was included to measure the effects of attention on undriven activity.

In some recordings, circular patches of 100% contrast, square waves were randomly interleaved with the Gabors to test responses to high-contrast stimuli that differed in average luminance from the background. The spatial frequency of the square wave was the same as the spatial frequency used for the Gabors, and the radius was set to 1.5 times the SD of the Gabor, so that they appeared to be about the same size. We used these particular stimuli because they had the same form as the Gabors and could be included in Gabor sequences without standing out as markedly different. When they were used, the square-wave stimuli were randomly inserted into the sequences of Gabors with the same timing. The square-wave stimuli were sometimes selected to be the target or distractor stimuli, so they had the same behavioral relevance to the animal as the Gabor stimuli.

During recording from a neuron, pairs of Gabors appearing on each side of fixation were selected so that each possible pairing of contrasts occurred equally often. Because the animal had to detect an orientation change, we forced the first pair of Gabors in each trial to have a readily visible contrast. The contrast of the target was randomly selected from all nonzero contrasts. In early recordings, the contrast of distractor stimuli (targets on the uncued side) was randomly selected from all nonzero contrasts, but in later sessions, it was always selected to be either a 100% contrast Gabor or a circular patch of 100% contrast square-wave grating.

Several features of the task were aimed at keeping the animal's attention as constant as possible. The use of exponentially distributed target times encouraged the animals to maintain constant vigilance throughout each trial. The brief, aperiodic stimulus presentations forced the animal to maintain attention on the cued side throughout the trial to avoid missing the appearance of the target, which often had a low contrast. Finally, the use of brief stimulus presentations made it unlikely that the animal could adjust his level of attention during the time that more challenging (low contrast) stimuli were presented.

Neurophysiological recording and analysis

After training was complete, a recording cylinder was implanted over V4 on the prelunate gyrus near the superior temporal sulcus at about the level of the dorsal end of the inferior occipital sulcus (Horsley-Clarke: 5 mm posterior and 12–15 mm dorsal). Data were collected from individual units in V4 in the left cerebral hemisphere of *monkey 1* and from V4 in both hemispheres of *monkey 2*. Recordings were made using transdural, extracellular, glass-insulated, Pt/Ir microelectrodes (~1 MΩ at 1 kHz). Signals were amplified, filtered, and monitored on oscilloscopes and an audio monitor. Action potentials were time stamped with 1 ms resolution using a window discriminator.

After spikes from a unit were isolated, its receptive field was plotted using hand-controlled visual stimuli presented while the animal maintained fixation. The preferred size and spatial frequency of a Gabor were then determined qualitatively, and these settings were used for all data collection from the unit. The stimulus locations were adjusted so that one series of Gabors fell on the receptive field of the neuron being recorded and the other was at an equal eccentricity on the opposite side of the fixation point.

Responses to the first stimulus in each sequence were excluded from analysis because these were forced to be a readily visible contrast and the animal might treat these stimuli differently because they could never be targets. We also excluded responses to target stimuli, stimuli appearing after target stimuli, and stimuli paired with a distractor. Responses to the 100% contrast square-wave gratings were not used in analysis except as noted.

Neuronal responses were measured by counting spikes within a period 50–200 ms after the onset of a stimulus. We used a brief sampling period to reduce the chance that counts would be influenced by the animal adjusting its attentional effort in response to stimulus contrast. Each contrast response function was based on neuronal responses to ≥12 repetitions of each contrast and a total of ≥100 stimulus repetitions for each attentional state.

Contrast response functions were determined for each attentional state using a weighted least-squares fit to a hyperbolic ratio function

$$r = r_{max} \cdot \left(\frac{c^n}{c^n + c_{50}^n} \right) + m$$

where r is the neuronal response, c is the contrast, r_{max} is the maximum attainable response, m is the spontaneous activity, c_{50} is the contrast at which response is half-maximal, and n is an exponent that determines the steepness of the response function. This function has been shown to provide a good fit to contrast response functions from visual cortex in cat and monkey (Albrecht and Hamilton 1982). To see whether the effects of attention were more consistent with contrast gain, response gain, or activity gain, we fit the data from both attentional states simultaneously using modified functions that included a term for attentional state. The contrast gain function (Fig. 1*C*) was

$$r = r_{max} \cdot \left(\frac{c^n}{c^n + a \cdot c_{50}^n} \right) + m$$

where a is 1 in the unattended state and assumes a different value for the attended state. The response gain function (Fig. 1*D*) also include a term a with the same properties

$$r = a \cdot r_{max} \cdot \left(\frac{c^n}{c^n + c_{50}^n} \right) + m$$

as did the activity gain function (Fig. 1*E*)

$$r = a \cdot \left[r_{max} \cdot \left(\frac{c^n}{c^n + c_{50}^n} \right) + m \right]$$

Some analyses were restricted to those neurons for which attention caused a statistically significant increase in activity. A neuron was considered to have a significant increase in activity if its responses to any contrast of the preferred orientation were significantly greater in the attended condition than in the unattended condition (1-sided Wilcoxon rank sum test, $P < 0.05$, with Bonferroni correction for multiple comparisons).

Analyses of correlation were made using Pearson's correlation coefficient. Statistical significance of correlations was assessed using the standard error of the z transform of the correlation coefficient, which was found by multiplying Fisher's r-to-z transform of the correlation coefficient by $\sqrt{df}$, where df is the number of degrees of freedom, equal to the number of contrasts sampled in both attentional states minus 3. Statistical significance was determined using a criterion of $P < 0.05$.

For some analyses the effects of attention were measured using a modulation index $(r_a - r_i)/(r_a + r_i)$, where r_a is the response when attention was directed toward the receptive field and r_i is the response when attention was directed elsewhere.

Receiver operating characteristic (ROC) analysis (Green and Swets 1966) was done using the same spike counts that were used for other analyses. ROC values were computed for each stimulus in both attention states by comparing the distribution of its spike counts with those collected during the presentation of the zero contrast stimulus in the same attentional state. ROC values for each attention state were fit separately with a Weibull function (Weibull 1951)

$$p = 100 - 50 \cdot e^{-\left(\frac{c}{\alpha} \right)^\beta}$$

where p is the neuronal performance (percent correct) and c is the contrast of the stimulus. The value of α is the contrast where neuronal performance is 82% correct. This contrast was taken as the detection threshold.

R E S U L T S

Complete data were collected from 131 individual V4 neurons (80 from *monkey 1* and 51 from *monkey 2*). Most receptive field centers were in the lower visual quadrant and ranged from 1 to 6° eccentricity. The median Gabor had a sigma of 0.3°.

Both animals did well at detecting orientation changes on the cued side and ignoring changes on the other side while these data were collected. When high-contrast targets appeared on the cued side, *monkeys 1* and *2* responded correctly on 95 and 96% of trials. As expected, detection was worse for targets of lower contrast. Counting only trials that ended with a correct response or a failure to respond, for targets with contrast of 100, 25, 6.3, and 1.6%, *monkey 1* was correct on 95, 92, 54, and 6% of trials, and *monkey 2* was correct on 96, 93, 57, and 0% of trials. Excluding trials that the animals ignored or on which they broke fixation, the overall percents correct were 52 and 64%. Both animals ignored stimuli on the uncued side, making eye movements to that side on no more than 1% of trials (either before or after a distractor stimulus appeared).

Neuronal responses to brief stimuli

Each stimulus appeared for only 94 ms so that there was little chance that the animal could adjust its attention in response to individual stimuli. Although single-unit studies do not typically use such short stimulus presentations, most V4 neurons responded well to these brief presentations (see also Luck et al. 1997). Figure 3*A* shows the responses of a representative V4 neuron to its preferred orientation in the attended condition, and the best-fitting contrast response function (see
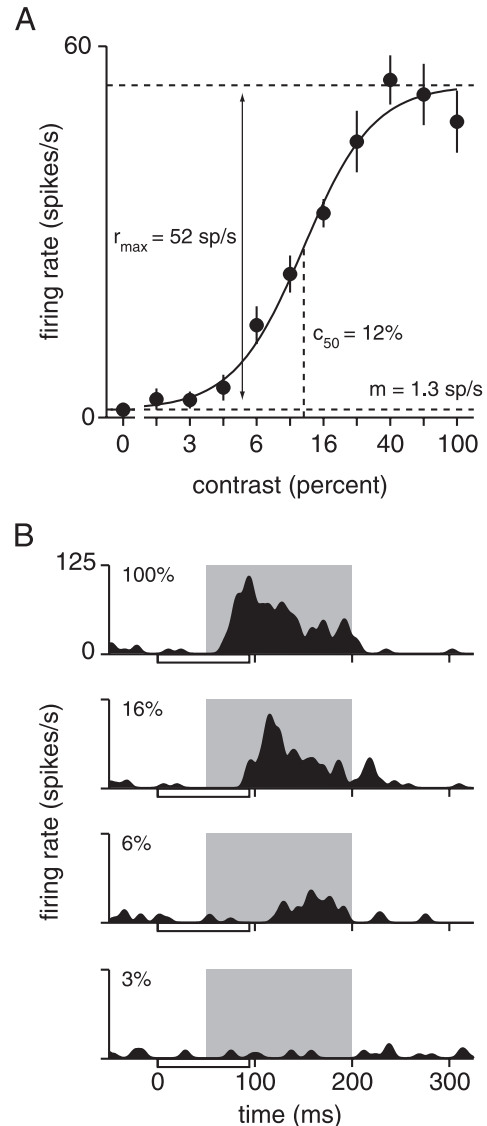

FIG. 3. Response of a representative V4 neuron to Gabors of different contrasts. Responses are to the preferred orientation and were collected while the animal had its attention directed toward the receptive field. Each point and histogram represents the average of ≥13 stimulus presentations. *A*: best-fitting contrast response function (see METHODS). The saturating values of the response function (m and $m + r_{max}$) are marked with horizontal dashed lines. The contrast producing a response midway between the saturating values (c_{50}) is indicated with a vertical dashed line. Error bars are ±1 SE. *B*: peristimulus time histograms of responses to selected contrasts. Each histogram has been smoothed with a Gaussian filter with a SD of 4 ms for display. The gray bands mark the 150-ms period during which spikes were counted in determining average firing rates. The bar under the *x* axis shows the time when the stimulus was present. Although the stimuli were brief, the neuron gave strong responses to moderate and high contrasts and yielded a well-formed contrast response function.

METHODS). The saturation values for the response function are marked with horizontal dashed lines. The spontaneous activity (*m*) for this neuron was 1.3 spikes/s. It responded strongly to stimuli of intermediate and high contrast, and its saturating response (r_{max}) was 52 spikes/s. The contrast that produced a half-maximal response (c_{50}) was 12%, which is marked with a vertical dashed line. The histograms in Fig. 3*B* show the average responses to selected contrasts as a function of time. The gray bands mark the period during which spikes were counted to determine average firing rates (50–200 ms). This period captured most of the response to the brief stimuli.

Figure 4 shows the distributions for the parameters from the best-fitting functions for all 131 cells. The fits were based on responses to the preferred orientation recorded while the animals directed their attention toward the receptive field. The median value of r_{max}, the maximum attainable response, was 31 spikes/s. For comparison, the median r_{max} for responses collected from macaque V1 in anesthetized animals using sustained drifting gratings was 27 spikes/s (Sclar et al. 1990), and the average response of V4 neurons in awake animals to a 500-ms presentation of a counterphasing Gabor was ~20 spikes/s (McAdams and Maunsell 1999a). The median value for the contrast producing a half-maximal response (c_{50}) was 15%, which indicates good contrast sensitivity. Neurons in anesthetized monkey V1 have less contrast sensitivity (higher c_{50}: 24%, Albrecht and Hamilton (1982); 33%, Sclar et al. (1990)). Greater contrast sensitivity in V4 probably arises from its larger receptive fields (Sclar et al. 1990; Watson 1992). The exponent, *n*, which determines the steepness of the contrast response function had a median value of 1.9, compared with 2.4 for V1 (Sclar et al. 1990).

Overall, these distributions show that V4 neurons provided good responses to the brief stimulus presentations used in this study. This is consistent with measurements from monkey V1 showing that the shape of the contrast response function changes little between the onset of a response and sustained portions (Albrecht et al. 2002). Also, the stimulus duration was not much shorter than typical fixation periods for unconstrained macaques (median 144 ms) (Gallant et al. 2000).

Effects of attention on responses to different contrasts: examples

We determined the effects of attention on V4 neurons by comparing average neuronal responses recorded when the animal directed its attention to the stimuli in the receptive field with those collected during interleaved blocks of trials when its attention was directed to the stimuli in the other hemifield. Figure 5 shows the effects of attention on the responses of three representative neurons. Each panel plots one cell's average response to Gabors with the preferred orientation but different contrasts; ● are responses collected during trials in which the animal's attention was directed toward the receptive field, and ○ are responses during trials in which the animal's attention had been directed to the other stimulus location. Like most V4 neurons, these cells responded more strongly when the animal's attention was directed toward the receptive field.

The average responses in Fig. 5*A* are stronger for all stimuli when attention was directed to the receptive field. High-contrast stimuli, which produced the strongest responses, were those for which attention produced the biggest change in firing rate, and there was an increase in the undriven firing rate (0% contrast). Thus the effect of attention on this neuron was most like an activity gain. The responses in Fig. 5*B* showed a different pattern in which the largest differences in firing rate occurred for intermediate contrasts with little effect on responses to the highest contrast, which is more like a contrast gain. Finally, the responses in Fig. 5*C* showed an uncommon pattern in which attention seemed to greatly enhance responses to intermediate contrasts so that responses to intermediate contrasts were stronger than responses to high contrasts when the animal paid attention to the receptive field but not when it attended elsewhere. The responses of this neuron are not easily described as activity gain, response gain, or contrast gain.
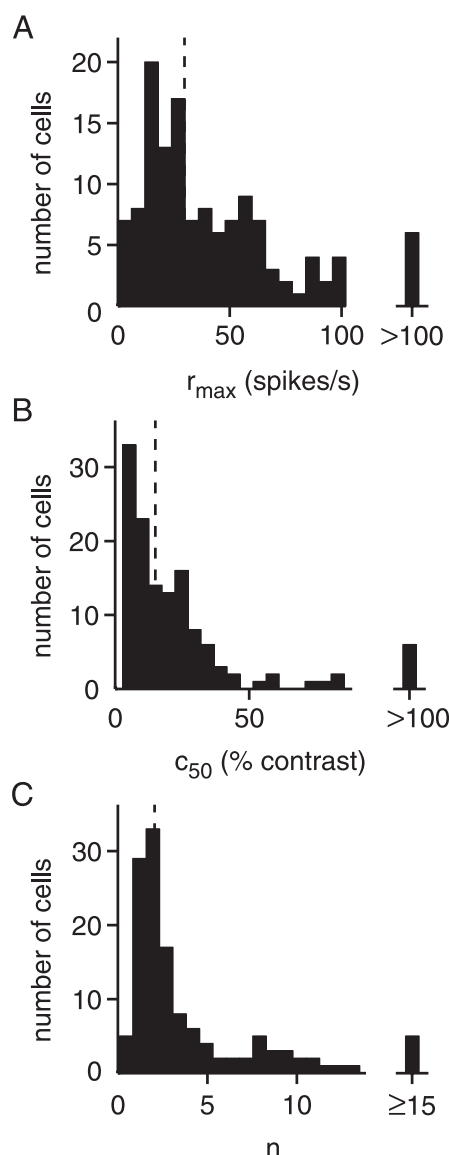
FIG. 4. Distributions of parameters from the contrast response functions fit to the preferred orientation responses in the attended condition for all neurons. Responses of each neuron were fit to a hyperbolic ratio function (see METHODS). *A*: values of r_{max}, which is the maximum attainable response. The median is 31 spikes/s. *B*: values of c_{50}, which is the contrast at which responses are half-maximal. The median c_{50} is 15% contrast. *C*: values of *n*, an exponent that determines how rapidly responses rise from baseline to saturation. The median value of *n* is 1.9. The median value for the parameter *m*, which reflects spontaneous activity, was 2.9 spikes/s (distribution not shown).
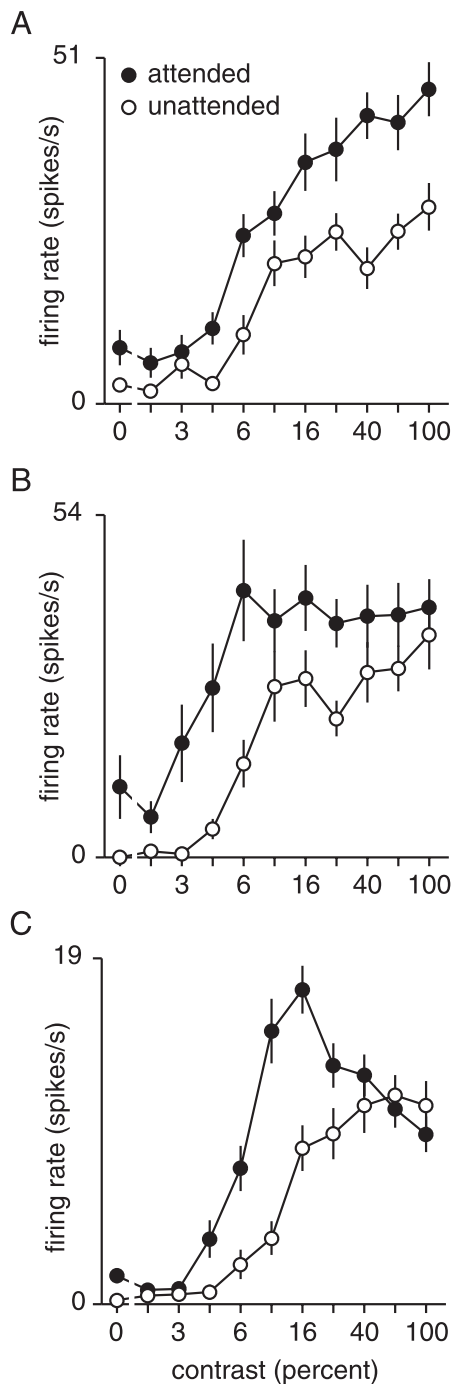
A

B

C

FIG. 5. Effects of attention on contrast response functions. Responses from 3 V4 neurons are shown. Responses were obtained using the preferred orientation for each neuron. ●, responses collected while the animal directed its attention toward the receptive field; ○, responses to the same stimuli that were collected while the animal directed its attention away from the receptive field. Error bars are ±1 SE. *A*: responses from a neuron for which the effect of attention was like an activity gain. *B*: responses from a neuron for which the effect of attention was like a contrast gain. *C*: responses from a neuron for which the effect of attention is not well described by any of the gain functions.

Effects of attention on responses to contrast: population

The overall effect of attention on V4 responses to different contrasts is illustrated in Fig. 6. Figure 6*A* shows the firing rate for different contrasts of each neuron's preferred orientation averaged across all 131 neurons. The average firing rate was greater for stimuli of all contrasts when the animal attended to the receptive field location (●) relative to when it attended to the distant location (○). Attention also affected average spontaneous activity (0% contrast), which increased from 5.3 to 7.5 spikes/s. The plot is not smooth because individual neurons were not all tested with every contrast, and some subsets of neurons had higher or lower firing rates, raising or lowering the average firing rate at particular contrasts. The same data are plotted in Fig. 6*B* after normalizing each neuron's firing rate to its strongest response to any contrast (which was not always 100% contrast, e.g., Fig. 5*C*). This normalizing reduced the sampling effects.

Neurons differ considerably in how much they are affected by attention. The effects of attention on contrast response functions can be seen more clearly by restricting the average to include only those neurons that were modulated by attention. Figure 6, *D* and *E*, shows the average firing rate and the average normalized firing rate for those neurons for which attention produced a statistically significant increase in firing (see METHODS, $n = 48$, 37%). These averages show that attention affected responses to all contrasts with the firing rate for high-contrast stimuli increasing as much or more than the firing rate for low or intermediate contrasts.

These average responses do not fit well with pure contrast gain, which predicts that there should be no effect of attention at the lowest contrasts and reduced effects at the highest contrasts. Contrast gain is most easily distinguished from activity and response gain at contrasts that are well into the high saturation of the contrast response function. In this saturated range, contrast gain predicts no effect of attention, while activity gain and response gain predict the largest effect. The responses that were significantly modulated by attention in Fig. 6, *D* and *E*, show the greatest change in firing rate at the highest contrasts, but these responses do not have pronounced high-contrast saturation. This is because some V4 neurons do not have strongly saturating responses (i.e., they have high c_{50}, see Fig. 4*B*). To examine the effects of attention in the high saturation part of the contrast response function, we looked at the average effect of attention on those cells with clearly saturating contrast response functions. Figure 6, *G* and *H*, plot the average responses of the subset of neurons that were significantly modulated by attention and also had responses that saturated at lower contrasts (c_{50} below median; $n = 19$, 15% of all neurons). This subset with clearly saturating contrast response functions shows pronounced effects of attention at the highest contrasts.

Effects of attention on contrast and orientation

Neurons were tested with at least two orientations for each contrast. Consistent with previous observations (McAdams and Maunsell 1999a), we found that attention had similar effects on stimuli of different orientations. Figure 6, *C, F,* and *I*, plots the average normalized firing rates for all contrasts for each neuron's null orientation (perpendicular to preferred). These responses are normalized to each neuron's firing rate for the contrast in the preferred orientation that produced the greatest response, so each plot has the same scaling as the plot in the row above. Striking effects of orientation are not expected because most V4 neurons are not strongly tuned for orientation. Gabor orientation typically modulates the responses only
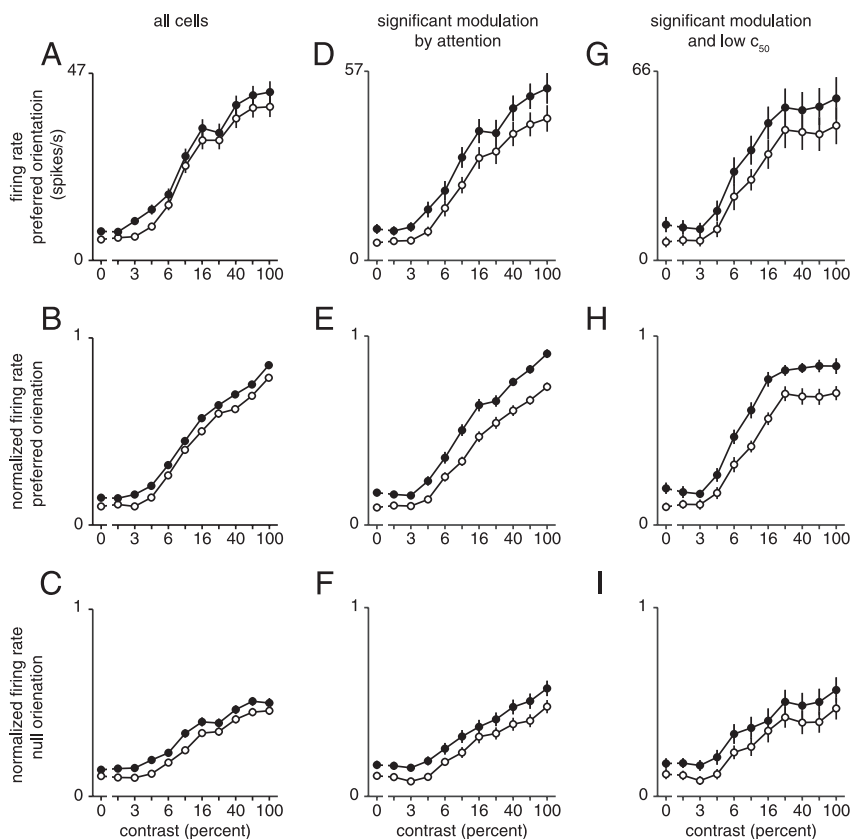
FIG. 6. Population contrast response functions. ●, responses in the attended condition; ○, responses in the unattended condition. Error bars are ±1 SE and are in some cases smaller than the symbols. Each panel plots responses as a function of contrast, but because different cells were tested with different contrasts, the number of cells contributing to different points varies. A–C: contrast response functions that include responses from all neurons recorded ($n = 131$). A: average firing rate in response to different contrasts of each neuron's preferred orientation. B: average response after normalizing to each neuron's strongest response. C: average responses to each neuron's null orientation, normalized to each cell's strongest response to its preferred orientation. D–F: corresponding plots for the subset of neurons for which attention caused a statistically significant increase in response ($n = 48$, 37% of all neurons). G–I: corresponding plots for the subset of neurons that were significantly modulated by attention and had a c_{50} lower than the median ($c_{50} <15\%$, $n = 19$, 15% of all neurons).

by about a factor of two (McAdams and Maunsell 1999a). Overall, responses to the null orientation are reduced relative to responses to the preferred orientation but otherwise have similar characteristics.

The effects of attention on responses to different contrasts and orientations are compared more directly in Fig. 7, A and B, which plots responses to attended stimuli against responses to the same stimuli when they were unattended. Dark gray sym-
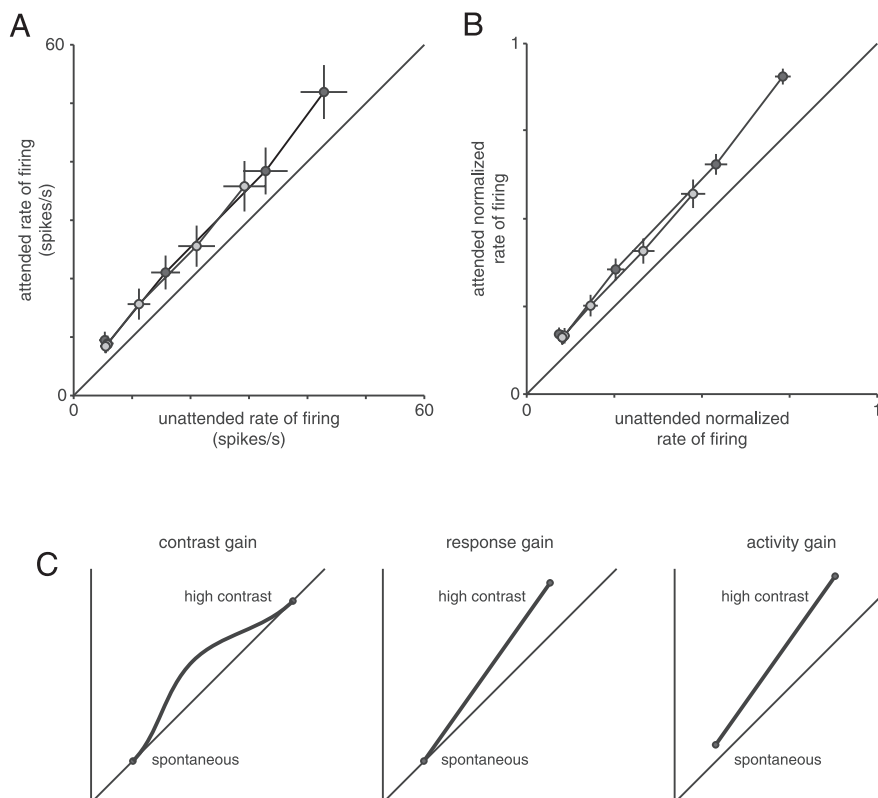

FIG. 7. Average effects of attention on responses to different contrasts and orientations. A: average firing rates for given contrasts and orientations in the attended and unattended condition. Dark gray points are responses to stimuli in the preferred orientation, light gray points are responses to stimuli in the null orientation. Lines connect points with different contrasts. B: same responses normalized to each cell's strongest response to its preferred orientation. Error bars are ±1 SE. Responses are averages from the 48 neurons with significant modulation by attention, and are only plotted for the 5 contrast levels that were tested for every neuron, with some points overlapping. C: schematics of how responses would be distributed if attention caused a pure contrast gain, response gain, or activity gain.

bols are responses to different contrasts of the preferred orientation, and light gray symbols are responses to the same contrasts of the null orientation. Figure 7A shows average firing rates, and Fig. 7B shows the same responses normalized to each neuron's strongest firing rate in response to a stimulus in the preferred orientation. The points lie above the diagonal because average responses were stronger for attended stimuli. Responses to contrasts in the null orientation (light gray) were weaker (closer toward the origin) relative to responses to the same contrast in the preferred orientation. The fact that points for both orientations fall on the same line shows that attention acted similarly on preferred and null stimuli; a given firing rate was modulated by the same amount whether that rate was in response to a low-contrast preferred orientation or a high-contrast null orientation.

The plots in Fig. 7, A and B, also shows that the effects of attention in this experiment are not perfectly described by any of the gain functions. The diagrams in Fig. 7C show how the different gain functions would be expected to distribute responses in these plots. Contrast gain would not modulate spontaneous activity or responses to the highest contrasts (i.e., those points would lie on the diagonal) and would have the greatest effect (departure from the diagonal) for intermediate contrasts. Response gain would not modulate spontaneous activity, so that point would remain on the diagonal, and other responses would lie along a straight line rotated around the point marking spontaneous activity. Activity gain would cause all responses to lie on a straight line passing through the origin.

The responses in Fig. 7, A and B, appear to fall on a straight line, as expected for response gain or activity gain. However, those lines do not match either model perfectly. Response gain predicts that spontaneous activity should fall on the diagonal, but a linear regression through the points in Fig. 7A places spontaneous activity (in the group of points nearest the origin) 3.3 spikes/s above the diagonal. Similarly, activity gain pre-

dicts that the line on which the points lie should run through the origin, the regression yields a y-axis intercept of 2.6 spikes/s. Thus none of the gain models is a perfect match to these average responses.

Effects of attention on responses to contrast: individual units

The data presented in Figs. 6 and 7 are averages across many neurons. To examine whether the effects of attention on individual neurons are well described by a particular gain model, we fit each cell's responses to stimuli in its preferred orientation with different contrast response functions (see METHODS). In the first analysis, the data from the attended and unattended conditions were fit separately, and we examined how attention affected the values of the best fitting parameters. Figure 8 shows the results of this analysis for the subset of 48 neurons that were significantly modulated by attention. For each parameter in the fitted functions we computed a modulation index, which compares its value in the attended and unattended conditions (see METHODS). A value of zero corresponds to no change, and values near 1 and −1 correspond to values that are much larger in the attended and unattended condition.

The average modulation indices were significantly greater than zero for r_{max} (15% increase) and m (a twofold increase). These parameters are related to the high and low saturation values for the contrast response function. The average proportional change was much larger for the lower saturation (spontaneous activity, see also Fig. 7). The average modulations of c_{50} and n were not significantly different from zero. Of the three models, only activity gain predicts that attention should increase r_{max} and m. However, activity gain predicts that r_{max} and m should change by the same proportion.

In another analysis, we fit the data from the attended and unattended conditions simultaneously. Figure 9 shows one example. Figure 9A shows the responses from one neuron and
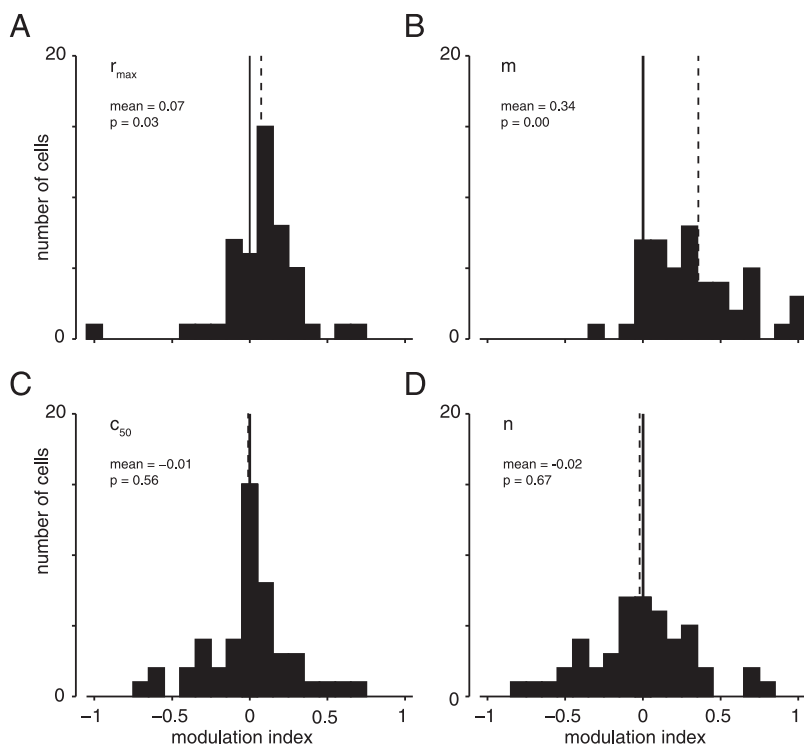

FIG. 8. Effects of attention on the fit of contrast response functions to neuronal responses. Each neuron's responses to stimuli of different contrasts in the attended and unattended states were fit separately with contrast response functions. Only neurons that were significantly modulated by attention were included in this analysis ($n = 48$). For each of the 4 contrast response function parameters (r_{max}, m, c_{50}, and n), the change between attention states was converted to a modulation index (see METHODS). Each panel plots the distribution for modulation of a particular parameter across the sample of cells, with dashed lines marking the mean modulation. The mean modulation was significantly different from zero for only r_{max} and m.
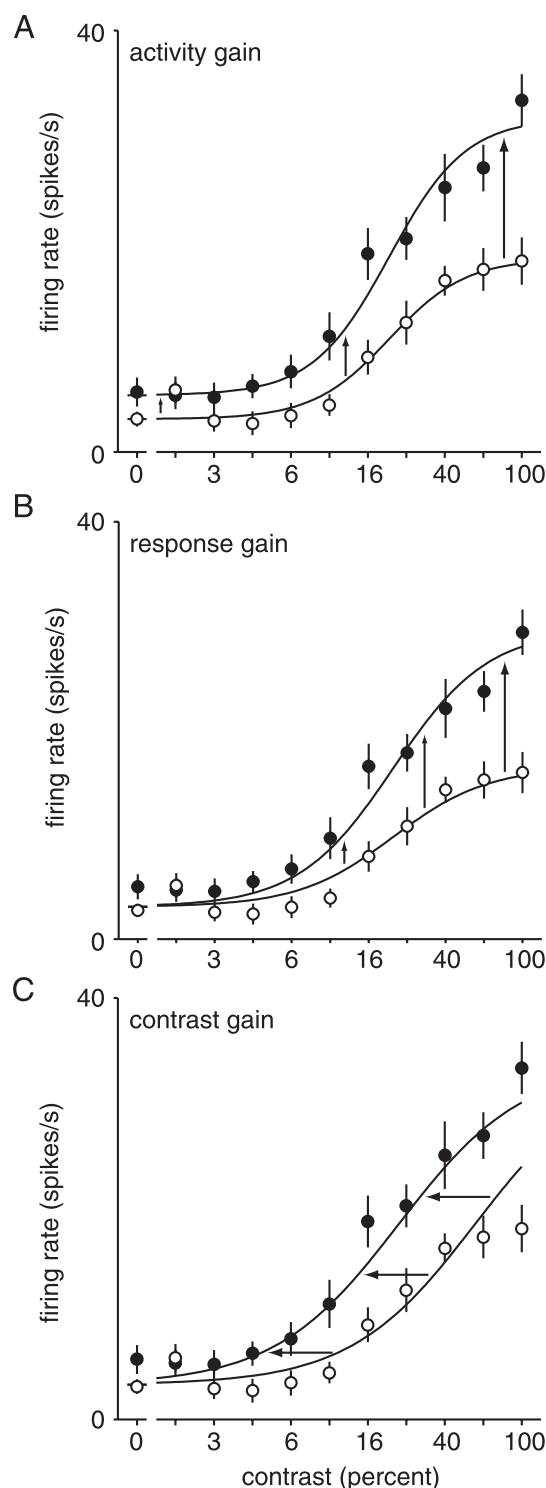
FIG. 9.   Responses from an example V4 neuron fit with the different gain functions. All 3 panels show the same responses, plotted in the same format as previous figures. Error bars are ±1 SE. *A*: best-fitting activity gain functions. The 2 curves differ by a single term that gives them different vertical scaling. The best fitting values for the unattended state were $r_{max} = 15.2$, $m = 3.1$, $n = 2.2$, and $c_{50} = 20.4$, and attention increased r_{max} and m by a factor of 1.73. *B*: best-fitting response gain functions. The two curves differ by a single term that increases the response without moving the lower saturation value. The best-fitting values for the unattended state were $r_{max} = 15.2$, $m = 3.5$, $n = 1.8$, and $c_{50} = 21.2$, and attention increased r_{max} by a factor of 1.98. *C*: best-fitting contrast gain functions. The 2 curves differ only by a single term that shifts them horizontally. The best fitting values for the unattended state were $r_{max} = 30.5$, $m = 3.3$, $n = 1.3$, and $c_{50} = 57.2$, and attention decreased c_{50} to 22.9.
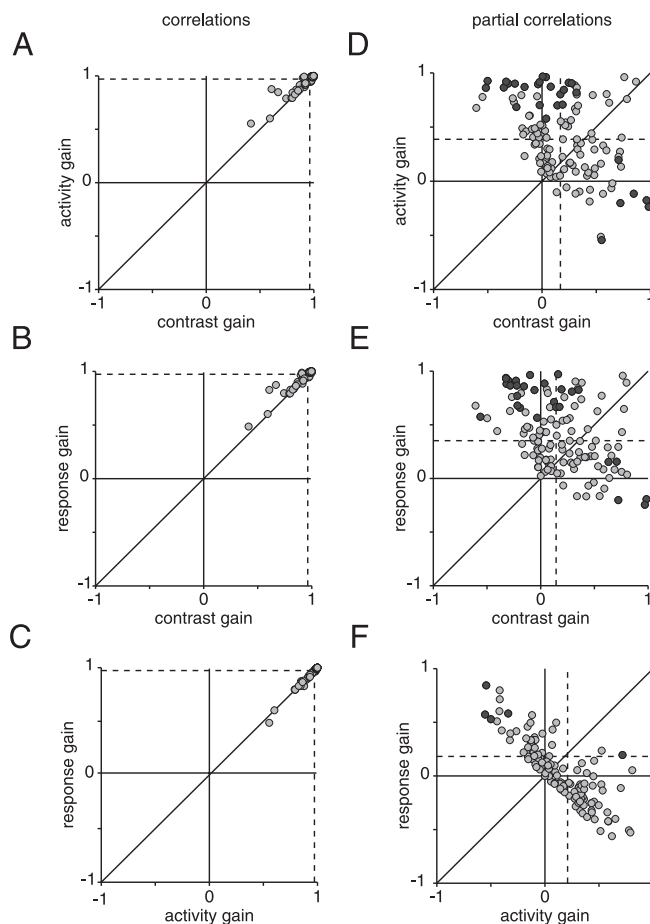

FIG. 10.   Correlations between the responses of each neuron ($n = 131$) and the different gain functions fit to those data. - - -, median for each measure. *A*: simple correlations between the average firing rates observed and values from the fitted functions for contrast gain and activity gain. *B*: contrast gain vs. response gain. *C*: activity gain vs. response gain. The median correlations for contrast gain, activity gain, and response gain are 0.98, 0.99, and 0.99. *D*: partial correlation between average firing rates and values from the fitted functions for contrast gain (median 0.17) and activity gain (median 0.39). The partial correlations eliminate effects from the strong correlation between the fitted functions. ●, values where the partial correlation for one function was statistically significant and significantly greater than the partial correlation for the other function ($P < 0.05$). *E*: partial correlations for contrast gain (median 0.14) and response gain (median 0.35). *F*: partial correlations between activity gain (median 0.21) and response gain (median 0.18).

the curves corresponding to the best-fitting activity gain function. The two curves were constrained to differ only by a single term that scaled them vertically, as indicated by the arrows (see legend). Figure 9*B* shows the same responses with the curves corresponding to the best-fitting response gain function, and *C* shows the responses fit with a contrast gain function. All the functions fit the data well, although in this case, the activity gain function fits the high- and low-contrast responses somewhat better.

Because each of the gain functions has the same number of free parameters, we can compare directly how well they describe the recorded responses. For each of the 131 neurons, Fig. 10, *A–C*, plots the correlation between actual responses and values from the best fits for contrast gain, activity gain, and response gain. The correlations were strong in every case. The median correlation coefficient for each function is marked with a dashed line. The median for contrast gain was 0.98, and the

medians for activity and response gain were both 0.99. These correspond to explaining 96 and 97% of the variance in mean responses across different contrasts and attentional states. Only a handful of cells had correlation coefficients <0.75. These high correlations show that the responses of neurons to different contrasts and attentional states could be well described by any of the functions. For example, the correlation between the responses and fitted curves in Fig. 9 is 0.99 for activity gain (*A*), 0.98 for response gain (*B*), and 0.97 for contrast gain (*C*).

The fits are all well correlated with the data because the gain functions all have a similar form and are therefore highly correlated with each other. We can look more closely at the response variance that is specifically explained by each fit by eliminating the effects of the correlation between the different functions. This is achieved using a partial correlation between the responses and each type of gain. Partial correlations of this sort have been used previously to examine whether the responses of direction selective neurons are better explained by models of pattern or component direction selectivity (Movshon et al. 1985; Smith et al. 2005). Figure 10, *D–F*, plots the partial correlations between each cell's responses and each pair of gain functions. Values are shown (●) where the partial correlation between the responses and one of the fitted functions is statistically significant and also significantly greater than the partial correlation between the responses and the other function (*P* < 0.05 for both tests, see METHODS). These plots suggest that the activity and response gain functions provide marginally better fits than the contrast gain function. For example, there are 22 units for which activity gain provides a significantly better partial correlation than contrast gain and only for 6 for which the converse is true (Fig. 10*D*). This slight bias in favor of activity gain is also seen in the medians for the partial correlations, which are marked (- - -). A similar result is obtained for response gain compared with contrast gain (Fig. 10*E*). The partial correlations for response gain and activity gain (Fig. 10*F*) are anticorrelated because these functions differ only in their behavior at spontaneous activity, and changes that improve the fit for one model typically adversely affect the fit for the other. Although there are hints that the data are better described by activity or response gain rather than contrast gain, each model provides an acceptable description of the data, and there is no basis for arguing that one is the correct choice. The points in the partial correlation plots are distributed continuously, suggesting that there are no segregated subsets of neurons that are much better explained by one model or another.

High-contrast stimuli

In an earlier study of the effects of attention on contrast response functions of V4 neurons, Reynolds et al. (2000) reported that attention preferentially enhanced responses to low contrasts, with relatively little effect on high-contrast stimuli, a pattern consistent with contrast gain. The current results instead suggest that the largest differences in firing rate occur at high contrasts and that the data are described at least as well by activity or response gain. Possible sources of this discrepancy are considered in the discussion. We consider here some specific measurements relevant to this difference.

Although our task and stimuli were similar to those used in the other study, there were some differences. The earlier study used sinusoidal gratings clipped to a rectangular window. Unlike Gabors, the windowed sinusoids contain relatively high spatial frequencies, abrupt luminance steps at their edges, abrupt changes in orientation, and a net increment or decrement in luminance relative to background when a noninteger number of cycles is windowed. Although we had no reason to believe that stimulus attributes such as these would affect attentional modulation, we wanted to test whether they might contribute to the discrepancy.

For the 51 neurons recorded from *monkey 2*, we included stimuli with some of the properties of those used by Reynolds et al. (see METHODS). Figure 11*A* shows the responses of one neuron that was tested with square-wave stimuli. Responses are shown when the animal's attention was directed toward (●) or away (○) from the stimulus in the receptive field. Responses to the square-wave gratings appear at the *right* of the plot. This neuron responded a little less well to the square-wave stimulus than to high-contrast Gabors, but the attentional modulation was similar.

Overall responses tended to be weaker for the high-contrast square-wave stimuli. Figure 11*B* plots each cell's response to the preferred orientation of the 100% contrast Gabor against its response to the same orientation of the 100% contrast square wave in the attended condition. The median response to a 100% contrast Gabor was 39.7 spikes/s, whereas that for the 100% contrast square wave was 23.3 spikes/s (- - -).

There was no evidence of systematic differences in attentional modulation for the high-contrast square wave. Figure 11*C* plots each neuron's attentional modulation index (see METHODS) for the 100% Gabor stimuli against the same index for the square-wave stimuli. There was no significant difference between the two indices (both means 0.06, or 13% modulation; *P* = 0.95 paired *t*-test). Thus we do not believe that the differences between our results and those of the other study arise from using windowed, high-contrast stimuli.

Neuronal detection of different contrasts

Although responses were stronger for stimuli in the attended location, the undriven firing rate was often elevated as well. This raises the question of whether there was net improvement in the detectability of stimuli. We examined this question by using ROC analysis to compare the performance of individual neurons in detecting stimuli of different contrasts with and without attention. Spike counts recorded in response to each stimulus were compared with spike counts from undriven activity (during the presentation of the 0 contrast stimulus) to derive a measure of how reliable neurons were at distinguishing the stimulus-driven activity from undriven activity (see METHODS). Responses to stimuli in each attentional state were compared with undriven activity from the same attentional state.

Figure 12, *A* and *B*, shows the results from one neuron. The plots in Fig. 12*A* show that this neuron's responses were appreciably stronger when the animal was attending to the stimulus in its receptive field (●) and undriven activity was elevated as well. The ROC analysis for these responses is plotted in Fig. 12*B*. This analysis effectively asks how often a random draw from spike counts recorded for each stimulus would be larger than a random draw from spike counts recorded when the zero contrast stimulus was presented. The
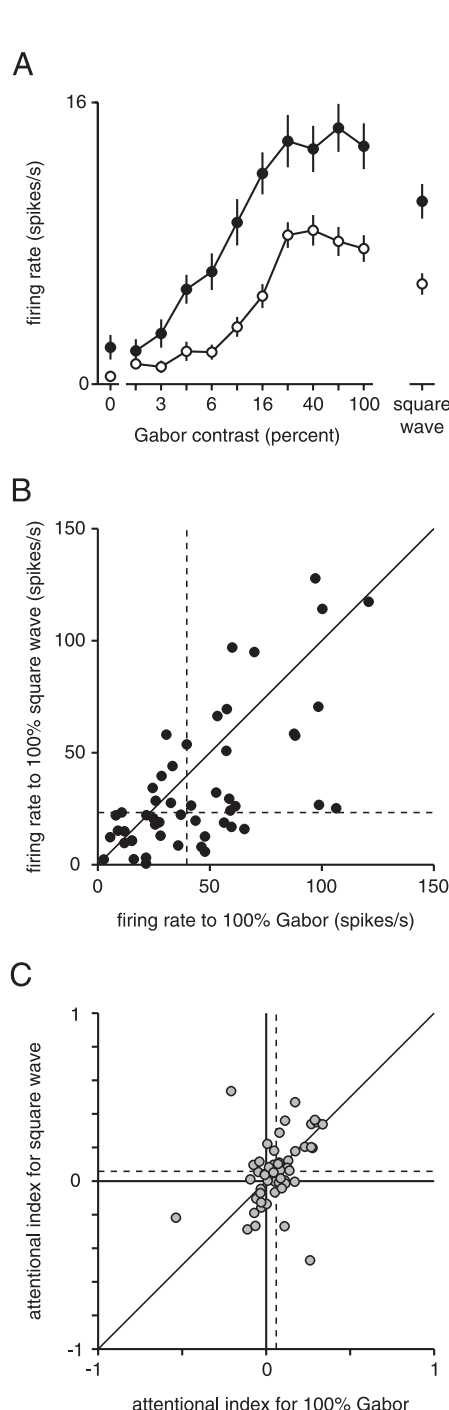
FIG. 11. Effects of using high-contrast square-wave grating stimuli. *A*: responses of a representative neuron that was tested with the usual Gabor stimuli and an additional high-contrast square-wave stimulus. ●, responses collected when the animal's attention was directed toward the receptive field; ○, when the animal's attention was directed away. Error bars are ±1 SE. The responses to the square-wave stimuli (*right*) were somewhat lower but showed about the same degree of attentional modulation. *B*: each neuron's average response to a 100% Gabor stimulus plotted against its average response to a 100% square-wave stimulus. Both responses were taken when the animal's attention was directed toward the receptive field. Neurons tended to respond better to the 100% Gabor stimulus. - - -, median responses. *C*: each neuron's attentional modulation index (see METHODS) for 100% Gabor stimuli plotted against the index for 100% square-wave stimuli. There was no significant difference in attentional modulation between the stimulus types.
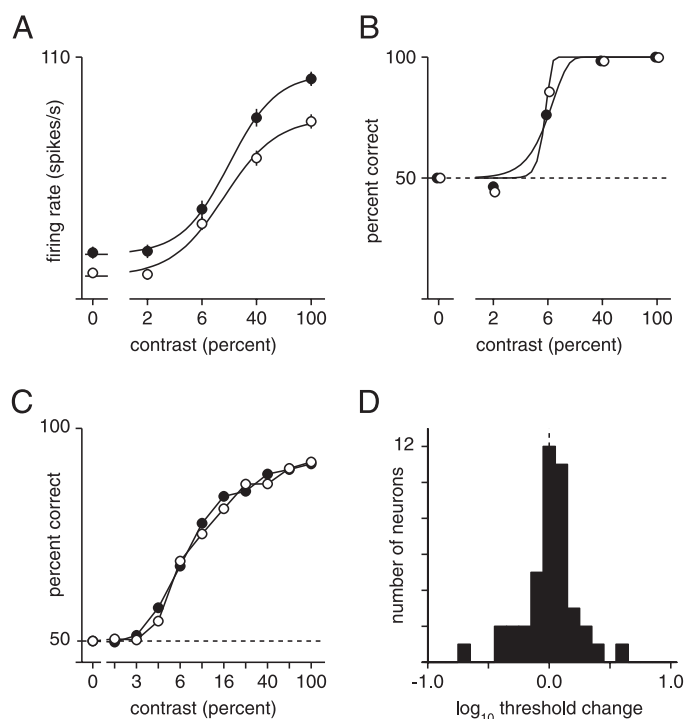

FIG. 12. Receiver operating characteristic (ROC) analysis. *A*: response of a representative neuron to different contrasts in the attended (●) and unattended conditions (○). *B*: ROC analysis of the responses in *A*. The increase in firing rate associated with attention did not improved performance. *C*: average ROC curves for the 48 neurons for which attention produces a statistically reliable increase in activity. On average, attention did not affect neuronal performance. *D*: distribution of changes in contrast threshold for attended and unattended ROC curves. Contrast thresholds were taken from functions fit to the attended and unattended ROC values for each neuron that contributed to *C*. When both thresholds were <100% contrast (42 neurons), the logarithm of the ratio of the contrast thresholds from the attended and unattended conditions was computed. The mean of the distribution is 0.013, which is not significantly different from 0.0 (*t*-test, $P = 0.71$). Thus no effect of attention on neuronal performance was detected.

ROC values for 0% contrast lie at 50% correct by definition. Although the neuron fired more spikes to the 2% stimulus when it was attended, the ROC values for that stimulus do not differ appreciably. This is because the undriven activity in the attended condition increased by as much as the response to the 2% stimulus, so the detectability of that stimulus did not improve. Additionally, while the biggest differences in firing rate occurred at the highest contrasts, these responses were nonoverlapping with undriven activity, so neuronal performance was saturated at 100%, and there was no difference between attended and unattended stimuli. (The slopes of the functions fit to the ROC values appear different, but this difference is not reliable, because the slopes are not well constrained with a single value between 50 and 100%.) Thus for this neuron changes in the rate of firing related to attention were not reflected by changes in ROC values.

Figure 12*C* shows average ROC functions for the attended and unattended conditions for the 48 neurons for which attention produced a statistically significant increase in firing. As seen for the example in Fig. 12, *A* and *B*, the values for attended and unattended conditions do not differ much. The ROC values from these neurons were also fit with a sigmoidal function to obtain a value for a contrast detection threshold (see METHODS). Six of these neurons had a threshold >100% and

were not considered further. For the remaining 42 neurons, the histogram in Fig. 12*D* plots the logarithms of the ratios of thresholds in the attended condition and unattended condition. The average value was 0.013, corresponding to a threshold in the attended condition that was at a contrast 1.03 times higher than the threshold in the unattended condition. This value is not significantly different from no change.

Two factors contributed to the lack of overall improvement in neuronal performance as measured by ROC analysis. First, although the neurons fired more spikes in the attended condition, for most units, the undriven activity in the attended condition also increased. The change in undriven activity was comparable to the change in driven rate for low contrasts (Figs. 5 and 6). Because driven and undriven activity both increased, low contrasts were not appreciably more detectable when the animal attended to the stimulus in the receptive field. Second, although attention caused the largest differences in driven rate at high contrasts (Fig. 6), neuronal performance was near saturation for high contrasts, so attention could not improve performance there. The combination of these effects left little effect of attention on neuronal performance across the range of contrasts.

These data should not be interpreted as meaning that attention cannot improve neurometric performance. To the contrary, attention has been shown to improve the performance of V4 neurons in other situations (McAdams and Maunsell 1999b; Reynolds et al. 2000). The current results rest on the assumption that detection depends on a comparison with current undriven activity, which may not be the case. If we compared all stimulus responses against undriven activity in the unattended condition, attention would improve the detection throughout the unsaturated portion of the ROC function. Furthermore it would be inappropriate to compare these neurometric plots with the animals' behavioral performance. The neurometric analysis measures how well neurons detected low-contrast stimuli, while the monkeys were required to detect changes in orientations. There is no reason to believe that individual neurons in V4 could provide reliable signals about differences in orientation when stimuli are drawn from a broad range of contrasts.

DISCUSSION

Earlier studies of V4 and MT suggested that the effect of attention on contrast response functions is like contrast gain: contrast response functions are shifted toward lower contrasts without substantial changes to the baseline or maximum response (Fig. 1*C*). The current data show instead that attention can have clear effects on these saturating portions of the response function. Unlike the previous studies, we found that the effects of attention on contrast response functions were marginally better explained as activity or response gain than as contrast gain.

Activity or response gain has not been ruled out

It is important to try to understand this discrepancy. One critical point is that although our results yield a qualitatively different conclusion, there is no evidence for a pronounced quantitative discrepancy. We found that all the gain functions explain our results well, based on the correlations between model fits and the data (Fig. 10, *A–C*). Martinez-Trujillo and Treue (2002) used a similar analysis to examine how well their data from MT were fit by contrast gain and response gain models and also found that both models provided an excellent fit: across the 34 neurons they examined, the correlation coefficients for both models were always >0.82 (i.e., ≥67% of the variance explained). Reynolds and his colleagues (2000) did not compare different gain models quantitatively, but the data presented (their Fig. 5) suggest that a quantitative assessment of the quality of fits would similarly have found that all three of the models provide a good description of the effects of attention. Although both of the earlier studies found that their data were better described as contrast gain, neither showed that activity or response gain were unacceptable descriptions or that contrast gain was much superior. Thus the effects of attention in all three studies may be described as contrast, activity, or response gain.

Further experiments will be needed to better characterize how attention acts on neuronal responses to different stimuli. The relative merit of the different models should become obvious if they are tested with neuronal responses that are much more strongly modulated by attention. Modulation of responses can be more pronounced when attention is shifted between two stimuli within a neuron's receptive field (Luck et al. 1997; Moran and Desimone 1985; Motter 1994a,b; Reynolds et al. 1999; Treue and Martinez-Trujillo 1999; Treue and Maunsell 1996, 1999), and it may be possible to use this approach with tasks that can ensure stable attentional allocation across different contrast conditions. Alternatively, attention typically modulates response to single targets more in later stages of visual cortex (Maunsell and Cook 2002), and it would be possible to exploit those stronger modulations if the more complex response properties in those regions could be accommodated (Miyashita 1993; Tanaka 1996).

Potential sources of differences between studies

Although there is no evidence for profound quantitative differences between the studies, we nevertheless need to consider why both the earlier studies found contrast gain to be somewhat better for describing the effects of attention. It is possible that the difference arises from subtle differences in tasks and stimuli, but we believe the most likely source of this discrepancy lies in differences in how attention was allocated for stimuli of different contrasts. Attention is dynamic, and the attentional modulation of neurons in visual cortex varies greatly with task demands (Boudreau and Maunsell 2001; Ghose and Maunsell 2002; Spitzer et al. 1988). If attention is allocated differently for high- and low-contrast stimuli, it can distort the difference between the attended and unattended contrast response functions.

For example, in the MT experiments of Martinez-Trujillo and Treue (2002), four stimuli were presented simultaneously. Two high-contrast stimuli with motion in the nonpreferred direction were always present inside and outside the receptive field. Each was paired with an adjacent, behaviorally irrelevant stimulus with motion in the preferred direction. Only the contrast of the behaviorally irrelevant stimuli was varied. This design might affect the way attention appears to act on high and low contrasts. If attention was always directed toward or away from both stimuli in the receptive field, there would be no

problem. However, as the irrelevant stimuli increased in contrast, they would become increasingly distracting, and subjects would be motivated to focus attention more on the adjacent, behaviorally relevant stimulus to reduce this distraction. Thus the spatial extent of attention might have been wide enough to include the distractor when it had low contrast but narrow enough to exclude the distractor on trials when it had high contrast. Because stimulus contrast was fixed throughout each trial, the animals could adjust their allocation of attention immediately after the stimuli appeared. If attention shifted between both stimuli inside the receptive field and both stimuli outside the field when distractor contrast was low (i.e., contributions from the null and preferred stimuli both modulated by attention), but attention shifted between the behaviorally relevant, nonpreferred stimuli when distractor contrast was high (i.e., null response modulated by attention, preferred response unmodulated), there would be relatively little attentional modulation of responses at high contrast even if attention acted with an activity gain mechanism. In addition to these potential effects of changes in the spatial distribution of attention, changes in the amount of attention directed to preferred and nonpreferred directions of motion could similarly affect results (Treue and Martinez-Trujillo 1999). Finally, in this study, contrast gain was compared only with response gain. It is possible that activity gain might have been somewhat superior to both.

The design of the Reynolds et al. (2000) V4 experiment was simpler. As in the current experiment, only one stimulus appeared inside the receptive field and one outside, so changes in the spatial distribution of attention cannot explain the difference between these results and ours. Instead, it may be that a difference arises from their animals paying more attention to low-contrast stimuli. Their task, like ours, required the animals to detect a target stimulus with a different orientation embedded in a sequence of other stimuli. However, their targets also had a different shape and a different size than other stimuli. Detecting these targets would be challenging primarily at low contrasts where the outline of the target would be difficult to assess. Several studies have shown that neuronal responses are modulated by attention to specific stimulus features, such as color, orientation or direction of motion (McAdams and Maunsell 2000; Motter 1994b; Treue and Martinez-Trujillo 1999). The animals in the experiment of Reynolds et al. (2000) would have been motivated to pay particular attention to low contrasts because only low-contrast targets would be difficult to detect. If contrast is treated as a feature like orientation or color, then it is possible that responses to low-contrast stimuli were more enhanced relative to high-contrast stimuli because the animals were paying particular attention to low contrasts. The existence of neurons in extrastriate cortex that are tuned to particular contrasts (Peng and Van Essen 2005) suggests that particular contrasts are treated as a stimulus feature in the visual system and might therefore be selected as a target for attention. Our animals were also challenged by low contrasts, but the effect might have been smaller because the orientation change of the Gabor was more difficult to detect at all contrasts. Thus they may not have attended so much to low contrasts.

We have no evidence that attention varied across contrasts in the other experiments, but stable attention is critical for comparing whether attention has effects that are more like contrast gain versus response or activity gain. This is not such a pressing issue when measuring the effects of attention on response functions such as orientation or direction tuning because different orientations or directions are approximately equally challenging. However, it is an important consideration for experiments on contrast response functions because low-contrast stimuli are always more demanding. Our experiments were designed with stable attention as a primary objective, and our overall results look less like contrast gain than the other experiments. It should be noted, however, that our design could not guarantee equal attention to all contrasts. Although the animals were challenged with detecting an orientation change, that orientation change was inevitably more difficult to detect at low contrasts, so the animals would have been motivated to direct more attention there. Were it possible to design a task that truly balanced task difficulty across contrasts, neurons might show responses that were even more like activity or response gain.

Effect of attention on undriven activity

The current results show that attention can increase the spontaneous activity of neurons in V4. This is consistent with previous studies of V4 that found that attention increases average spontaneous activity by a few spikes per second (Luck et al. 1997; Reynolds et al. 2000). An earlier study from our laboratory did not see a change in spontaneous activity when spatial and featural attention were shifted (McAdams and Maunsell 1999a). The absence of an effect in that experiment was probably an artifact of task design. In that experiment, animals did a match-to-sample task in which the stimuli were presented for relatively long periods (500 ms) that had perfectly predictable timing. The subjects had no motivation to direct attention to the receptive field until after a stimulus appeared. Consistent with this, average attentional modulation was negligible at the beginning of stimulus presentations and grew during the stimulus presentation. The effect of attention on spontaneous activity was measured in a period immediately before the first stimulus presentation when the subjects may not have directed their attention to the cued location.

There are hints that the effects of attention on undriven activity may to some extent be independent of its effects on driven activity. The data in Fig. 7A fall on a straight line that intercepts the y-axis above zero; this is not expected for any of the models considered here. It is as if attention to the receptive field location added a few spikes per second of activity on top of a multiplicative effect on driven activity. A similar offset was seen in the effect of attention on V4 responses to different orientations (McAdams and Maunsell 1999a; Fig. 4B), but in that case, it was a reduction of a few spikes per second. Additionally, Luck and his colleagues (1997) found that attention increased undriven activity in V4 without a detectable effect on driven rate.

The current data show that attention modulated undriven firing rates and weaker responses by a greater proportion than strong responses. This effect might arise from an interaction between attentional modulation and response transients. It has been noted that attentional modulation may be reduced during a strong transient response compared with either later periods in a response or weaker response onsets (Womelsdorf et al. 2001). Relatively little is known about the dynamics of attentional modulation during various phases of sensory responses.

Attention and activity gain

Although previous reports suggested that the action of attention on contrast response functions is a contrast gain mechanism, the current results indicate that it is premature to dismiss activity or response gain in favor of contrast gain as a description of the effects of attention on sensory neurons. It remains possible that the primary mechanism by which attention acts may be an overall increase in sensitivity that increases responses to all stimuli by a similar proportion as would arise with activity gain. Although we emphasize that the current data do not favor any of the models, because the activity gain model has been discounted in earlier reports, we wish to emphasize that it remains viable and to point out that it has attractive features.

For one, activity gain might be simpler to implement. Together with earlier studies (McAdams and Maunsell 1999a; Treue and Martinez-Trujillo 1999), the current data show that attention modulates strong and weak responses by approximately the same proportion when differences in response are caused by changes in orientation or direction. This effect of attention could be explained by an overall increase in sensitivity of the neurons being recorded, such that the effects of attention on responses to different contrasts, orientations and directions (indeed all stimuli) arose from a single mechanism. This possibility is illustrated in Fig. 13, in which firing rates in the unattended condition (lower curves, ○) are all increased by the same proportion regardless of what combination of orientation and contrast produced the firing rate. If attention acts on contrast response functions through a mechanism of contrast gain, it would require a more elaborate mechanism in which the effects of attention are adjusted depending on the overall level of activity within a population of neurons.

Several observations hint that the activity gain model may ultimately be shown to be an acceptable description of the effects of attention. The current data and other studies have shown that attention can affect undriven activity, so activity gain is likely to provide a more complete description than response gain and contrast gain, which predict no effect on spontaneous activity. It is difficult for a pure contrast gain mechanism to explain effects of attention that have been seen with stimuli of 100% contrast in areas like MT (Cook and Maunsell 2002, 2004; Seidemann and Newsome 1999; Treue

and Martinez-Trujillo 1999; Treue and Maunsell 1996), where values of c_{50} are typically so low that most neurons would not be expected to show any modulation if attention acted by contrast gain (Sclar et al. 1990; Thiele et al. 2000). Some studies have failed to see attentional modulation with a single high-contrast stimulus in the receptive field (Desimone et al. 1985; Recanzone and Wurtz 2000), but these do not represent strong support for contrast gain because attentional modulation depends on how challenging a task is (Boudreau and Maunsell 2001) and the precise demands of that task (see Seidemann and Newsome 1999).

The form of modulation of neuronal response that would be needed for activity gain has been widely observed in sensory processing independent of attention, and several neuronal mechanisms for implementing it have been described (Albrecht and Geisler 1991; Carandini and Heeger 1994; Chance et al. 2002; Salinas and Sejnowski 2001; Salinas and Thier 2000). Thus it is possible that attention may act through gain control mechanisms that are similar to those used by feed-forward sensory processing. Future studies will be needed to establish whether the effects of attention are best described by activity gain.

Psychophysical studies

Several psychophysical studies have examined how attention affects behavioral performance for stimuli of different contrasts, with inconsistent results. One study reported that effects of attention on psychometric functions are more like response gain (Morrone et al. 2004), another found effects more like contrast gain (Carrasco et al. 2004), whereas another found evidence for both response gain and contrast gain (Huang and Dobkins 2005). Ling and Carrasco (2006) recently reported that although the effects of sustained attention on psychometric functions look like contrast gain, those of transient attention look like a combination of contrast gain and response gain. These investigators suggested that some of the differences between these reports arise from a difference in how attention was manipulated in the various experiments, which seems likely.

Psychophysical studies do not provide strong constraints for understanding how attention affects the contrast response functions of neurons. Given the uncertainties about the steps intervening between neuronal firing rate and behavioral performance, any of the effects of attention on response to different contrasts considered here might underlie a particular psychophysical result. Even the effects of attention on neurometric functions based on ROC analysis of responses to different contrasts (Fig. 12, Reynolds et al. 2000) do not provide direct insights into how attention affects contrast response functions based on firing rates. Because neurometric functions are constrained by high and low saturations at 100% performance and chance, they transform the effects of activity or response gain into a primarily horizontal shift along the ROC contrast axis, making them difficult to distinguish from the effects of contrast gain. An understanding of how attention affects neuronal responses will probably require further direct examination of the firing rates of individual neurons.
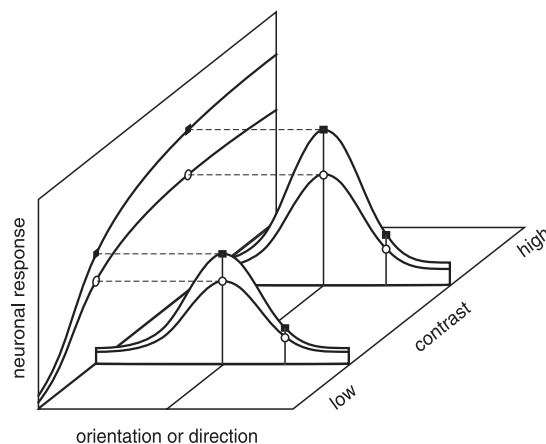

FIG. 13. Hypothetical activity gain for both contrast and orientation or direction. Although the illustrated effect is activity gain, the effects of response gain would differ only slightly. See text for discussion.

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