Chapter 4: Additive effects of attention and stimulus contrast in primary visual cortex

Summary

Previous studies have proposed a variety of mechanisms by which attention influences neuronal activity. Here we investigated the mechanisms of attention in the striate cortex of monkeys performing a spatial or an object based attention task at various stimulus contrasts and compared neuronal contrast response functions with and without attention. Our data are best described by an additive interaction: the influence of attention on the neuronal response is relatively independent of the stimulus contrast, at least when the stimulus has enough contrast to become visible. This shows that attention adds to the neuronal responses in a largely contrast invariant manner. These data support recent fMRI studies, and suggest that feedback from higher areas exerts a constant attentional drive that is mostly task not stimulus driven.

Introduction

Our ability to detect and discriminate a visual stimulus improves when we direct our attention to it, especially if the stimulus is faint or embedded in a cluttered scene (Bashinski and Bacharach, 1980; Dosher and Lu, 2000; Lu and Dosher, 1998; Zenger et al., 2000). Over the last 2 decades it has become clear that attention shifts are associated with changes in the activity of neurons in the visual cortex as well as in subcortical structures. Neurons that respond to an attended object increase their firing rate while the neuronal responses to other, unattended objects are suppressed. The attentional modulation of neuronal firing rates in cortex was initially described in higher visual areas (Bisley and Goldberg, 2003; Bushnell et al., 1981; Moran and Desimone, 1985; Reynolds et al., 1999; Spitzer et al., 1988; Treue and Maunsell, 1996), but later also in low-level visual areas including the primary visual cortex (Ito and Gilbert, 1999; Li et al., 2004, 2006; Motter, 1993; Roberts et al., 2007; Roelfsema et al., 1998; Vidyasagar, 1998).

Despite a wealth of studies, important questions about the mechanism by which attention influences neuronal activity have remained unresolved. Some previous studies showed that attention scales neuronal responses in proportion to the response in the absence of attention: weak responses increase slightly while strong responses increase more (McAdams and Maunsell, 2000; Treue and Maunsell, 1996; Treue and Trujillo, 1999). The findings inspired a ‘multiplicative’ or ‘response-gain control’ model of attention (Figure 1A). However, this
response gain model may not hold for all stimulus features, as the effects of attention and stimulus contrast on a neuron’s response do not always interact in a multiplicative manner.

Specifically, Reynolds et al. (Reynolds et al., 2000) demonstrated that attention enhances the weak response of neurons in area V4 evoked by low contrast stimuli, but that it has only little influence on the stronger response evoked by high contrast stimuli (Figure 1B). Attention thus appeared to shift the neurons’ contrast response function to the left, as if it increased the effective contrast of the stimulus in their receptive field. In a subsequent study, Martínez-Trujillo & Treue (Martinez-Trujillo and Treue, 2002) showed that neurons in motion sensitive area MT behave similarly: they also shift their contrast response function when the stimulus in their receptive field is attended, in support of what is now called the ‘contrast-gain model’ of attention. The idea emerging from these studies is that attention and contrast share the same neuronal code (Treue, 2004). This hypothesis received support from a psychophysical study in human observers showing that an attended stimulus appears to have a higher contrast than a stimulus that is not attended (Carrasco et al., 2004).

The idea that the effects of attention are similar to an increase in stimulus contrast is not undisputed, however, as one psychophysical study reported that attention has only little influence on perceived contrast (Prinzmetal et al., 1997), while another study demonstrated that attention and contrast can even have opposite effects (Roberts and Thiele, 2008a, 2008b). Furthermore, observers are well able to direct their attention to low contrast image regions, and even give them priority if they are task relevant (Einhauser et al., 2008; Pashler et al., 2004). Also, a recent neurophysiological study by Williford and Maunsell (Williford and Maunsell, 2006) found that attention does not necessarily result in a change of contrast gain of area V4 neurons. They observed that some neurons exhibited features of attention induced contrast gain changes, while other neurons changed their response in accordance with the response gain model, and yet others displayed mixed effects. These results, taken together, suggest that attention and contrast may interact in multiple ways, but a single unifying picture has not yet emerged.
Imaging studies using fMRI in human observers inspired yet another type of model for the interaction between attention and contrast. In higher visual areas, such as the fusiform face area, the strength of the neuronal responses is relatively independent of the stimulus contrast once the stimulus has the necessary contrast to be perceived (Avidan et al., 2002). These contrast invariant responses are only observed, however, for attended objects while the responses evoked by unattended objects depend monotonically on stimulus contrast (Murray and He, 2006). If the attentional modulation of neuronal responses in lower visual areas depends on the feedback from higher areas, then it might be expected that the attentional modulation of neurons in low level areas is also relatively independent of contrast. Recent fMRI studies (Buracas and Boynton, 2007; Murray, 2008) observed precisely such an **additive** interaction between attention and contrast in lower level visual areas V1, V2, and V3:

**Figure 1. Three models for the effect of attention on contrast response functions**

(A) According to the response-gain model, attention increases the response in proportion to the response evoked in the absence of attention. The dashed curve represents the contrast response function without attention, the continuous curve the contrast response function with attention, and the dotted curve shows the response difference. Note that the effect of attention on neuronal firing rates is predicted to be strongest at the highest contrasts.

(B) Contrast-gain model that proposes that attention increases the effective contrast, causing a leftward shift of the contrast response function. This model predicts strongest effects of attention on the neuronal responses evoked by stimuli of lower contrast.

(C) The additive model proposes that attention adds a fixed amount to the neuronal response once the stimulus has sufficient contrast to be detected by the animal. In this model the effect of attention is relatively constant across a wide range of stimulus contrasts.
attention added an amount of BOLD activity that did not depend strongly on stimulus contrast (Figure 1C).

In an attempt to reconcile these discrepancies we investigate the effect of attention on contrast tuning in the primary visual cortex of monkeys. We chose V1 as our target area because the previous electrophysiological studies on the interaction between attention and contrast were carried out in extrastriate areas. We conjectured that if attention and contrast are effectively interchangeable in affecting neuronal responses in area V1, at the lowest hierarchical level of visual cortical processing, then this type of interaction might be inherited by higher visual areas. Additionally we specifically intended to test the possibility of an additive interaction between attention and contrast. Figure 1 illustrates that the predictions of the additive model are intermediate between the predictions of the contrast-gain and response-gain models. The response-gain model predicts that attentional modulation is strongest for stimuli with a high contrast, the contrast-gain model predicts strongest modulation at low contrast, while the additive model predicts relatively constant effects across a range of contrasts once the stimulus has enough contrast to become visible. To ensure the generality of our results, we studied the effects of attention in the primary visual cortex with two different tasks, a detection task probing aspects of top-down spatial attention and a curve-tracing task which probed aspects of object-based attention.

**Methods**

All experiments were carried out in accordance with the European Communities Council Directive 1986 (86/609/EEC), and the US National Institutes of Health Guidelines for the Care and Use of Animals for Experimental Procedures. The experiments performed at Newcastle University were additionally approved by the UK Home Office and in accordance with the UK Animals Scientific Procedures Act. Those performed at the Netherlands Institute for Neuroscience were approved by the institutional animal care and use committee of the Royal Netherlands Academy of Arts and Sciences.

**Surgical preparation**

Experiments at Newcastle University: Following initial training, monkeys were implanted with a head holder, eye coil, and recording chambers above V1 under general anesthesia and sterile conditions. All details regarding surgical procedures, postoperative care and the cleaning of the implant and recording chambers are published in detail elsewhere (Thiele et al., 2006).
Experiments at the Netherlands Institute for Neuroscience: Two macaque monkeys were implanted with a head holder and a gold ring was inserted under the conjunctiva of one eye for the measurement of eye position.

In a separate operation, arrays of 4x5 or 5x5 electrodes (Cyberkinetics Neurotechnology Systems Inc.) were chronically implanted in area V1. The operations were performed under aseptic conditions and general anaesthesia. Details of the surgical procedures and the postoperative care have been described elsewhere (Roelfsema et al., 1998).

**Behavioural tasks**

We employed two different tasks to determine the effect of attention on contrast response functions in V1. In one of the tasks the animal’s attention was directed by a visual cue on each trial. Their task was to detect a subtle change in luminance of the test stimulus presented at the cued location. We will refer to this task as the ‘detection task’ for the remainder of the paper (Figure 2A). These experiments were conducted at Newcastle University. In the other task animals had to perform a mental curve tracing task, in order to determine which of three peripherally located circular targets was connected to the fixation point. We will refer to this task as the ‘curve tracing task’ for the remainder of the paper (Figure 2B). The curve tracing experiments were conducted at the Netherlands Institute for Neuroscience. We obtained behavioural and neuronal data from two animals in each of the two tasks, thus providing data from a total of four animals.
Figure 2. Two tasks used to investigate the effect of attention on contrast response functions in area V1. (A) Detection task. Monkeys grasped a touch bar and fixated a fixation spot (FP) at the centre of the monitor. After 250 ms of fixation, a cue was displayed indicating where the animal should attend (here we illustrate an attend RF trial). The cue was on for 400 ms, thereafter a period of 250 ms (monkey B) or 900 ms (monkey H) followed in which the animal maintained fixation until the test stimuli (black bars) appeared that had a varying luminance contrast. After an additional 500-800 ms a small patch with a higher luminance appeared either at the cued location (in which case it was a target) or at the distracter location. The animal had to report the target appearance by releasing the touch bar, but to ignore distracter appearances. Dashed circle: receptive field (RF). (B) Curve-tracing task. The monkey fixated a red fixation point (FP) in the centre of the screen. After 300 ms three curves with three red circles at their ends were displayed. The monkey had to trace the target curve (T) that was connected to the fixation point and to ignore the distracter curves that were not connected (D), while he maintained fixation. Either the target curve or distracter curve fell in the RF. After a delay of 500 ms the fixation point disappeared and the monkey made an eye movement to the circle at the other end of the target curve (blue arrow).
Detection task:

Monkeys had to detect a small change in luminance at a cued (attended) location, while ignoring a luminance change that occurred at a non-cued location (Figure 2A outlines the basics of the task). Monkeys initiated trials by holding a touch bar and fixating a red fixation point (FP, 0.1° diameter) on a grey background (21 cd/m²) presented centrally on a 20” analogue CRT monitor (75 Hz in monkey B, 100 Hz in monkey H, 1,600 x 1,200 pixels, 57 cm from the animal). The eye fixation window was ±0.3° - 0.35° in monkey B and ±0.6° - 0.7° in monkey H. Eye position was recorded with a scleral search coil in monkey B and with a scleral search coil or an infrared based camera system in monkey H (Thomas Recording GmBH). A cue (blue annulus, 0.24° outer diameter, 0.18° inner diameter) was presented for 400 ms on one side of the fixation spot along the (invisible) line connecting the FP and the RF location. The cue was displaced either towards or away from the RF, at a distance from the fixation point of one quarter of the eccentricity of the neuron’s RF to indicate whether attention should be directed towards or away from the stimulus presented in the RF, respectively. After cue offset, a 250 ms blank (900 ms in monkey H) period occurred with just the FP present. Spatial and temporal separation of the cue from the test stimuli ensured that it had no direct effect on the neuronal response to the test stimulus. Thereafter, two identical stimuli were presented (test stimuli), one centered on the RF, the other at the same eccentricity in the opposite hemi-field. Test stimuli were bars of the neuron’s preferred orientation and subtended 0.4° x 0.1° of visual angle. The luminance of the bar was parametrically varied to measure the contrast response function when animals attended to the neuron’s RF and when they attended away. We used 8 different contrasts, which were: 5.3%, 9.9%, 14.6% 20.4% 25.4% 30.4%, 49.5%, and 100% Michelson contrast. The luminance of the bars was lower than the background, i.e. a 100% contrast refers to a black bar on a grey background. After 500-800 ms (randomized in 1 ms steps) a brighter patch (0.1° x 0.1°) appeared at the centre of one of the bars. If presented in the cued location it is referred to as ‘target’, if presented in the non-cued location it is referred to as ‘distracter’. The target and distracter were brighter than the test stimuli and brighter than the background. The brightness difference to the test stimuli depended on the test stimulus contrast. The brightness difference to the background was constant. This means that behavioural performance in the detection task does not reflect the monkey’s ability to detect the bar itself, but to detect the target on top of the bar. Expressed in Michelson contrast the brightness difference of the target to the background was 4.3% for monkey B and 23.1% for monkey H. After the presentation of a target, the monkey had to release the touch bar within 500 ms to receive a juice reward. If a
distracter was presented first the monkey had to continue to hold the touch bar and maintain fixation until target appearance, which was 1,000-1300 ms (randomized in 1 ms steps) after distracter appearance. If the monkey made no response, the trial was terminated 500 ms after presentation of the target or distracter, whichever appeared last. Touch bar releases (correctly or incorrectly) or failure to maintain fixation resulted in immediate trial termination. For each stimulus contrast the target occurred once at 500-800 ms after bar onset (early target condition) and once at 1,000-1,300 ms after distracter onset (late target condition).

Attentional cueing was done in a blocked design; blocks were counterbalanced in random order. Conditions of cueing towards the location of the RF are labeled ‘attend-RF’, conditions of cueing attention towards the opposite hemifield are labeled ‘attend-away’. Conditions (early or late target) were presented in pseudorandom order within each block. If the monkey made an error the condition would be repeated later in the block. Twenty trials per stimulus and attention condition were recorded in most recordings. Cells were excluded if fewer than 10 trials per stimulus and contrast were available.

Curve tracing task:

The monkeys sat at a distance of 75 cm from a monitor (CRT monitor, 21", with a resolution of 1024 × 768, and frame rate of 75 Hz). The eye position was monitored with the double induction technique (Bour et al., 1984) and sampled at a rate of 900 Hz. A trial started as soon as the monkey’s eye position was within a 1° × 1° window centered on the fixation point (0.2° diameter). After an interval of 300 ms, circular targets (0.6° diameter) and curves appeared on the screen but the monkey had to maintain fixation (Figure 2B). The background display was grey (luminance 16.3 cd/cm²), the circular targets and the fixation point were red and the curves were darker than the background. The contrast of the curves was parametrically varied between 2% and 100% Michelson contrast (2%, 4%, 8%, 12%, 18%, 24%, 48%, and 100%).

In each trial three curves were presented (Figure 2B), one of the curves was the target curve that was connected to the fixation point. The other two curves that were not connected to the fixation point were distracters. Within a trial, all the points (pixels) of the three curves had the same contrast, and only differed in their connection to the fixation point. After 500 ms, the fixation point disappeared and the monkey made an eye movement to one of the larger circles. An eye movement to the circle at the end of the target curve was counted as correct and rewarded with apple juice. Eye movements to the other circles were counted as errors and no reward was given. Trials in which the monkey failed to maintain fixation until the
disappearance of the fixation point were terminated immediately. We presented four stimuli in an interleaved fashion. The stimuli shown above each other in Figure 2B are identical except for the connection to the fixation point. For one stimulus of such a pair the RF of the multi-unit recording site was on the target curve and for the other stimulus it was on the distracter curve. In our analysis, we pooled the neuronal responses across the two stimuli with the RF on the target curve and across the two stimuli with the RF on the distracter curve. Note that the stimulation of the classical RF is the same for the responses evoked by the target and distracter curve. All stimulus conditions (4 stimuli at the eight contrast levels) were randomly interleaved and were presented equally often. In a recording session we recorded at least 30 correct trials for every stimulus.

Assessing behavioral performance
To determine behavioral performance and stimulus visibility as a function of contrast we fitted the following Weibull function to the psychophysical data of our monkeys:

\[
\text{Visibility}(c) = \text{Perf}_{\text{max}} - (\text{Perf}_{\text{max}} - 0.5) \ast e^{-\left(\frac{c}{\alpha}\right)^{\beta}}
\]  

(1)

In this function \(\text{Perf}_{\text{max}}\) corresponds to the performance at the highest contrasts, \(c\) are the different contrast levels used, \(\alpha\) is the threshold contrast and \(\beta\) determines the slope of the function.

Neuronal data analysis
Due to the different nature of the recorded signals (discrete single unit spikes in the detection task and multi-unit activity in the curve tracing task) the initial processing differed for the two data sets. For the detection task, spike times in relation to stimulus and behavioural events were analysed and converted into spike frequencies within periods of interest. These single trial spike frequencies were used for the statistical assessment of contrast sensitivity functions and the effects of attention on neuronal activity. The MUA recorded in the curve tracing task is a continuous signal. We calculated peri-stimulus time histograms (PSTHs) for the various contrast and attention conditions in a time window from 500 ms before stimulus onset until 1000 ms thereafter, and smoothed these PSTHs with a 5-point moving average (5 data points correspond to 6.58 ms) to measure the peak response (Pe) that occurred when the stimulus of the highest contrast was presented. We computed the average spontaneous activity (Sp) in a window of 300 ms to 0 ms before stimulus onset, and normalized the responses by first subtracting Sp and dividing the result by the peak response.
We applied the same normalization to the activity on single trials for the statistical assessment of the contrast sensitivity functions and to quantify the effects of attention on neuronal activity in the curve tracing task.

Receptive field mapping

The receptive fields and orientation tuning of single units that were recorded in the detection task were characterized before the main task. The receptive fields were mapped by presenting a 0.1° black (100% contrast) square at pseudo-random locations on a 10x10 grid (i.e. a 1° x 1° area; 5 repetitions at each location; 100 ms presentation time with 100 ms gaps), while monkeys fixated centrally on the CRT. To prevent the monkey from attributing a ‘special status’ to the RF location, an identical stimulus was simultaneously presented in the opposite hemifield. The resulting space dependent response distributions were displayed online to determine the RF location. Stimuli used in additional cell characterization and the contrast tuning function were presented at the centre of the RF.

For monkey B the preferred orientation was measured by varying test stimuli orientations in 8 steps of 22.5° between 0° and 157.5° (stimulus size: 0.4° x 0.1°, 100% contrast) while the monkey performed the detection task as described above. Each stimulus was presented 8 times for both attention conditions. The preferred orientation was taken as the orientation with the highest mean response in either attention condition. In monkey H we determined the preferred orientation (in conjunction with the preferred spatial frequency and phase) by employing a reverse correlation technique (DeAngelis et al., 1994; Ringach et al., 1997). Stimuli were 336 circular patches of static sinusoidal gratings (1.0° diameter) varying in orientation (12 orientations 0-165 °), spatial frequency (1, 3, 5, 7, 8, 9, 10 cycle/°) and phase (0, 0.5π, π, 1.5π). Gratings were presented for 60 ms in a pseudo-randomized order centred over the receptive field. Responses were averaged over a 60 ms time window following stimulus onset at + 30 ms, and at + 60 ms. 5-10 repetitions of each stimulus were averaged. The stimulus that yielded the peak response was taken to represent the preferred orientation.

The MUA that was recorded in the curve tracing task provides an instantaneous measure of the number and the size of action potentials of neurons in the vicinity of the electrode tip (Super and Roelfsema, 2005). MUA represents the pooled activity of a number of single units in the vicinity of the tip of the electrode, and the population response obtained with this method is expected to be identical to the population response obtained by pooling across single units. We recently compared MUA to single unit data in the curve tracing task, and found that the signal provides a reliable estimate of the average single-unit response (Super
We obtained recordings with sufficient signal-to-noise ratio from ~75% of the electrode sites. For these sites, receptive field dimensions were measured by determining the onset and offset of the visual response to a slowly moving light bar, for each of the eight movement directions (Super and Roelfsema, 2005). The median area of the receptive fields was 0.8 deg² (range 0.12 deg² to 3.9 deg²). Receptive field eccentricity ranged from 0.9° to 4.4° with an average of 2.5°.

**Statistical assessment of stimulus driven responses and attentional effects**

To determine whether neurons responded (differently) to the different stimulus contrasts and whether attention had a significant effect on neuronal activity we used the single trial data averaged over the period from 200-500 ms after stimulus onset for each cell (site) as previous studies demonstrated that attentional effects in V1 and V4 neurons are most pronounced during the sustained response phase (Reynolds et al., 2000; Roberts et al., 2007; Roelfsema et al., 1998). We then performed a 2-Factor ANOVA to determine whether stimulus contrast (Factor 1) or attention (Factor 2) significantly affected neuronal activity, and whether there was an interaction between the two factors. Only cells (sites) that showed a significant effect of contrast on firing rates were included in the study.

**Determination of contrast sensitivity and modeling of contrast response functions**

To investigate whether the effect of attention on the contrast response function was best described by a contrast-gain, response-gain or an additive model, we adopted and modified an approach introduced by Williford and Maunsell (2006), who fitted functions to the contrast response functions of the following general form:

$$R(c) = R_{\text{max}} \times \left( \frac{c^n}{c^n + c_{50}^n} \right) + M,$$

where $R(c)$ is the response as function of contrast, $R_{\text{max}}$ is the saturated response, $c_{50}$ is the contrast at which the half maximal response is reached, $n$ determines the slope of the contrast response function, and $M$ corresponds to the spontaneous activity. We used multidimensional unconstrained nonlinear minimization (Nelder-Mead) to minimize the summed squared difference between the data and the model (Matlab 7.1, Mathworks). The above model has been shown to provide a good approximation of contrast response functions in monkey visual cortex (Albrecht and Hamilton, 1982; Thiele et al., 2004; Williford and Maunsell, 2006).
To determine the effect of attention on contrast tuning we fitted three different models to the data. The contrast-gain model holds that attention increases the effective contrast, and was modeled as follows:

$$R(c, a) = R_{\text{max}} \left( \frac{c^n}{c^n + a \cdot c^{50^*}} \right) + M,$$

where $a$ determines the effect of attention on the shift of the contrast response function (i.e. the effect on $c50$). Using this function, we performed a combined fit to the data from the attend RF and attend away conditions where $a$ was the only difference between the two attention conditions.

We also determined whether the response gain model gave an adequate description of the effect of attention on the contrast response function, by fitting the following function:

$$R(c, a) = a \cdot R_{\text{max}} \left( \frac{c^n}{c^n + c^{50^*}} \right) + M$$

Thus, the response gain model holds that attention ($a$) increases the response magnitude by a constant factor.

As a third model we fitted the additive model, which assumes that attention adds a constant amount of activity to the neuronal response once the stimulus has sufficient contrast to become visible:

$$R(c, a) = a \cdot \text{Visibility}(c) + R_{\text{max}} \left( \frac{c^n}{c^n + c^{50^*}} \right) + M$$

where stimulus visibility was determined independently by fitting equation 1 to the animals’ behavioral performance (the visibility function was rescaled so that it ranged from 0 to 1). The term \text{Visibility} was derived individually for monkey B, G, and A from fitting equation (1) to the performance data. Since in monkey H performance was fairly constant across all contrast levels (for reasons described in the Results section), we used the \text{Visibility} function from monkey B (who performed the same task as monkey H) to fit neuronal data from monkey H.
To determine which of the models describes the effect of attention best, we calculated the percent variance accounted for, and Pearson’s correlation coefficient between the data and the model. Given the similarity of the different models, we calculated the partial correlation coefficient, i.e. the correlation of the data with the model after taking into account the effect of the comparison model. Partial correlations were calculated as previously described (Movshon et al., 1985; Smith et al., 2005).

Results

Behavioral performance

The performance of the animals in the two different tasks as a function of stimulus contrast is shown in Figure 3. The animals were proficient in both tasks, provided the stimulus had sufficient contrast. In the detection task, the performance of monkey B fell to ~50% correct at low contrast, because the luminance increment was difficult to detect if the test bar contrast was low (Figure 3A). This effect was not observed in monkey H because this animal had to detect a luminance increment that was well above the background luminance (23.1% Michelson contrast), and he could even successfully complete the task in the absence of test bars visibility. Behavioural contrast threshold was quantified by fitting a Weibull function to the performance data (see Methods). For monkey B the threshold contrast ($\alpha$) was 11.03%, while the slope of the curve ($\beta$) was 3.03. Due to the relatively constant performance of monkey H, a Weibull fit was not performed. The performance of the two monkeys in the curve tracing task fell to chance level at low luminance contrast (Figure 3B), because this task could not be solved when the curves were difficult to discriminate from the background. Quantifying stimulus visibility by fitting equation 1 to their average performance revealed threshold values of 7.85% and 5.58% respectively and slopes of 28.7 and 1.44.
Neuronal data from the detection task

In the detection task we recorded from 109 cells that were well driven by the higher contrast stimuli (41 cells from monkey B, 68 from monkey H). The RFs of the neurons were located in the lower quadrant, at an eccentricity of 2°-7°. Figure 4A illustrates data from a typical recording session. The response of the example V1 cell increased as a function of the stimulus contrast, while attention also influenced the responses: the neuronal activity was stronger when attention was directed to the stimulus inside the RF than when attention was directed to the stimulus in the opposite hemifield. For this example neuron, the effects of attention were observed across all the contrast levels above 10%, i.e. the contrast levels where the test bar was easily perceived.

Figure 3. Performance as a function of stimulus contrast.

(A) Performance of the two animals in the detection task on trials that were not aborted due to a fixation break. Note that performance of Monkey B fell to chance level for test bars of low contrasts, because the luminance increment was difficult to detect. In monkey H, the performance was also good with low contrast bars because the luminance increase relative to the background was higher and could even be detected in the absence of the test bar.

(B) Performance of the two animals in the curve tracing task on trials not aborted due to a fixation break. The performance fell to chance level for the lower contrasts because the animals could not do the task if the curves
To investigate whether the effect of attention on the contrast response function was best described by a contrast-gain, response-gain or an additive model, we fitted our data from the 200-500 ms response period with the 3 different models outlined in Methods. It can be seen for the example shown in Figure 4B that the contrast gain model captured some aspects of the contrast response function, but failed to account for attentional effects at higher contrasts.

**Figure 4. Activity of V1 neurons in the detection task.**

(A) Example cell that showed an increased response when attention was directed to the receptive field. Note that the influence of attention is most pronounced in the sustained response phase, after the initial response transient evoked by the appearance of the test bar in the RF. (B) Average activity of the neuron in A evoked by test bars of various contrasts that were attended (red) or not attended (blue). We fitted the data with a contrast response function individually (individual fits), and with a contrast gain model, a response gain model, and an additive model. Error bars show S.E.M. VA denotes the percentage of variance accounted for by each of the three models. (C) A second example V1 neuron in the detection task.
luminance contrast (especially at 50% and 100% contrast). The fitted functions accounted for 94.5% of the variance in the data. The response gain model gave slightly better fits to the example cell. The fits of this model to the contrast response functions accounted for 97.7% of the variance (Figure 4B). The additive model gave the best description of the effect of attention on the contrast response function and accounted for 98.1% of the variance in the data.

Figure 4C shows another example neuron that was recorded in the detection task. It can be seen that also for this neuron, the additive model accounted for most of the variance in the data, closely followed by the response-gain model, which in turn, gave a better description of the data than the contrast-gain model. Although the additive model explained the largest amount of variance in the data, it is worth emphasizing that the two alternative models were by no means poor model descriptors, both explaining at least 82% of the variance for the two example neurons. Similar results were obtained for the entire data set, i.e. the amount of variance explained by the different models was generally fairly large (usually >70%).

**Population analysis**

Attention significantly altered the response of 18 of 41 (43.9%) cells from monkey B, and 37 of 68 (54.4%) cells in monkey H in the detection task. Given that we are interested in the effects of attention on the neuronal responses, we focused our analysis on cells that were significantly affected by attention. We wished to determine which of the models provides the best fit across the population of cells. It is convenient that the three models have the same number of free parameters, so we can directly compare the quality of the fits. The examples of Figure 4 illustrated that all three models provided reasonable fits to the data, and we therefore focused our analysis on the extra variance that one of the models can account for when the predictions of one of the other two models are taken into account. To this end, we calculated partial correlations (Movshon et al., 1985; Smith et al., 2005; Williford and Maunsell, 2006) which are shown in Figure 5A. The upper panel compares the pair-wise partial correlations between the contrast-gain and the response-gain model. Points along the ordinate represent neurons that were best described by the response-gain model, while points along the abscissa correspond to neurons best fitted by the contrast-gain model. It can be seen that the partial correlations of the response gain model were on average much larger than those of the contrast gain model (p<0.001, rank sum test). Thus, the response-gain model gave a better account of the effect of attention on the contrast response functions than the contrast-gain model.
Figure 5. Population analysis of the detection task.

(A-C) Distributions of partial correlations between fits of two models. A) comparison of the contrast-gain and response-gain model. Abscissa (ordinate), residual correlation coefficient between contrast-gain (response-gain) model and data after the correlation between the data and response-gain model (contrast-gain) is taken into account. The medians of the distributions are indicated by the numbers next to the dashed lines. Black dots denote data points where partial correlations were significant for one model and significantly larger than the partial correlations for the comparison model (p<0.05). P-values denote whether the distributions of partial-correlation coefficients were significantly different from another (rank-sum test). B) Comparison between the contrast-gain model and the additive model. C) Comparison between the additive model and the response-gain model. (D) Average responses in the detection task evoked by the attended (dashed curve) and unattended test bars (continuous curve) of varying contrasts. Error bars show SEM. Black stars denote data points where the activity in the attend RF condition was significantly stronger than the activity in the attend away condition (p<0.05, Wilcoxon signed rank test). The lower panel shows the absolute activity difference (thick grey curve, ordinate to the left) as well as the proportional difference, i.e. the response difference divided by the activity in the attend RF condition (black curve with ordinate on the right).
The middle panel (Figure 5B) presents the equivalent comparison between the contrast gain model and the additive model. It can be seen that the additive model also gave a better fit to the data than the contrast-gain model. The final comparison was between the response-gain model and the additive model, and it is shown in Figure 5C. The additive model gave significantly better fits to the data than the response gain model (p=0.03, rank sum test). The same finding held true if partial correlations were calculated on all cells, irrespective of whether they were significantly affected by attention or not (p<0.001, rank sum test).

We next computed the contrast response functions with and without attention by averaging across the activity of all the significantly affected neurons (Figure 5D). Attention increased the responses at medium as well as at high contrast levels. This result is not compatible with the contrast gain model, which predicts that the effects of attention are small for stimuli with a high contrast, and thereby supports the findings from the partial correlation analysis. The lower panel of Figure 5D shows the absolute and proportional response difference caused by attention. The absolute difference (grey curve) increased with luminance contrast and reached a plateau at 20% luminance contrast, while the proportional change (dashed curve) reached a peak at 20% luminance contrast, and showed a slight decrease at the higher contrasts.

Influence of attention on ongoing activity

There is a variant of the response gain model called ‘activity-gain model’ that proposes that attention also increases the ongoing activity (Williford and Maunsell, 2006). A number of previous studies in extrastriate visual cortex reported that attention increases the ongoing activity in addition to its effect on stimulus driven activity (Luck et al., 1997; Williford and Maunsell, 2006). To the best of our knowledge no such effect has been reported for area V1. We therefore compared the ongoing activity in the attend RF and attend away condition. Interestingly we found that attending to the RF actually slightly but significantly reduced the ongoing activity (ongoing activity attend away: 2.34+/- 3.44 spikes/sec; attend RF: 2.09+/- 3.07 spikes/sec; p<0.003; paired t-test). This implies that the activity-gain model cannot give a better account of our data than the response-gain model, and we thus did not consider it further.
**Curve tracing task**

Previous studies gave conflicting results on how attention influences contrast response functions, with some studies supporting the contrast-gain model and others supporting the response-gain model. Our analyses so far revealed that the additive model significantly outperforms the contrast and the response gain models. We decided that it is important to replicate this result with another task to investigate the generality of these findings, and we therefore studied neuronal responses in area V1 during a curve-tracing task.

**Figure 6. Activity in area V1 in the curve-tracing task.**

(A) Responses evoked at a MUA recording site in area V1 by target and distracter curves of varying contrasts during the curve-tracing task.

(B) Average activity in window from 200-500 ms evoked by the target (red symbols) and distractor curves (blue symbols). The red and blue curves represent best fits contrast response functions fitted individually (left panel), of the contrast-gain model, the response-gain model and the additive model (right panel). VA, the percentage of the variance accounted for by each of the models.
In the curve tracing task we recorded from a total of 38 multi-unit recording sites in area V1 (15 sites in monkey G, 23 sites in monkey A) with RFs at eccentricities ranging from 0.8° to 4.5°. Figure 6A illustrates the responses evoked at an example recording site by curves with various levels of luminance contrast. It can be seen that the response amplitude increased with contrast, and also that the target curve generally evoked stronger responses than the distracter curve. The attentional modulation was pronounced at the higher contrast levels and basically absent when the curves had a very low contrast so that they were hardly visible. Accordingly, the contrast-gain model did not fit the contrast response functions as well, although it still accounted for 94.7% of the variance (Figure 6B). The response-gain model fitted better (96.8% explained variance), while the additive model gave the best fit to the data (97.4% explained variance).

Across the population of recording sites, the effects of attention were widespread in the curve-tracing task, as the responses at 23/23 (100%) of the recording sites in monkey A and at 15/15 (100%) of sites in monkey G were significantly modulated by the difference between the target and distracter curve. We compared the three models by computing the partial correlation coefficients that are shown in Figure 7A. The results of this analysis were in line with the data from the detection task. The additive model gave the best fit to the data and it significantly outperformed the response-gain (p<0.001, rank sum test) as well as the contrast gain-model (p=0.0085, rank sum test). The response-gain model, in turn, gave a better fit to the data than the contrast-gain model (p=0.0098, rank sum test).

We next computed the contrast response functions at the population level, by averaging across the responses evoked at individual recording sites (Figure 7D). It can be seen that attention increased the activity across all contrast levels, although a small peak in the effect of attention can be seen at ~10% contrast. The difference in the response between target and distracter curve reached a plateau at ~20% contrast. The dashed curve in Figure 7B shows the proportional change in the response due to attention. The proportional changes were largest at low luminance contrast (the peak proportional change of 70% occurred at 2.6% luminance contrast), and decreased to a level between 15% and 20% at ~8% luminance contrast. The dependence of the proportional change on stimulus contrast is in accordance with the poorer fit of the response gain model, which holds that the proportional increase is relatively independent of contrast.
So far we tested the predictions from three models of attentional modulation, and assumed that only one of the three models was at work. It is possible that attention acts to increase the contrast gain as well as amplifies the response. Such a model would require additional fitting parameters. The reason for the additional parameter is that attention increases the Rmax value while it decreases the c50 value in the contrast gain model, i.e. a single fitting parameter cannot account for both simultaneously. Due to the additional fitting parameter it is not

Figure 7. Population analysis of neuronal responses in the curve-tracing task.

(A-C) Partial correlations between neuronal responses and models for the effects of attention on contrast response functions. A) compares the contrast-gain and response-gain model. Abscissa (ordinate), remaining correlation coefficient between contrast-gain (response-gain) model and data after the correlation between the data and response-gain model (contrast-gain) has been taken into account. B) Comparison of the contrast-gain model to the additive model, and C) comparison of the response-gain model to the additive model. The additive model gave the best fit, followed by the response-gain model, which in turn fitted better than the contrast-gain model. Median partial correlations are indicated by dashed lines and the adjacent numbers. P-values denote whether the distributions of partial-correlation coefficients were significantly different from another (rank-sum test). Black dots denote data points where partial correlations were significant for one model and significantly larger than the partial correlations for the comparison model (p<0.05). (D) Average neuronal activity evoked by the attended (dashed line) and unattended curve (continuous line) in the curve-tracing task for stimuli with various contrasts. Error bars denote SEM. Black stars denote data points where attention significantly enhanced
Possible to calculate/compare the partial correlations in an unbiased manner. However, we were able to compare the normalized Chi² values that were obtained by fitting the different models to our data (Chi² normalized by the number of fitting parameters) (Roberts et al. 2007). We found that the combined contrast- and response gain model yielded significantly larger normalized Chi² values than the additive model in both data sets (p<0.05, RM-ANOVA on ranks), while it was not significantly different from the simple contrast gain or the response gain model. This additional analysis shows that the additive model is also a better descriptor of the data than a combined contrast-response gain model.

Discussion

Here we have investigated how attention influences contrast response functions in area V1. We used two different behavioral paradigms to ensure that our results did not depend on the specific demands of the task at hand. Our results are clear and consistent across the two tasks: attention increases neuronal firing rates in area V1 at low and high stimulus contrast, and the additive model gives a better description of our results than the contrast-gain and response-gain models. We anticipated to find robust effects of attention at the higher contrast levels, because we and others have used high contrast stimuli to study the neuronal correlates of attention shifts in area V1 (Motter, 1993; Roberts et al., 2007; Roelfsema et al., 1998; Vidyasagar, 1998). However, we now found that the effects of attention on the responses evoked by low to medium contrast stimuli in area V1 are equally strong, and we conclude that the effects of attention on the V1 firing rates are relatively independent of luminance contrast, at least once the stimulus has sufficient contrast to become visible (once animal performance reaches ~ 82% detection).

Comparison to studies proposing contrast-gain and response-gain models

Although our results are not in accordance with previous neurophysiological studies on the effect of attention on contrast response functions, we feel confident about the validity of our results that were obtained with two different behavioral tasks. We noted in relation to Figure 1 that the predictions of the additive model are intermediate between those of the contrast-gain and response-gain models. The previous neurophysiological studies focused on the contrast gain and response gain models, and did not consider the possibility of an additive interaction. A predominance of additive effects may, however, also provide an explanation for the variable results obtained in previous studies in area V4 that tried to distinguish between the response-gain and contrast-gain models (Reynolds et al., 2000; Williford and Maunsell,
2006), and it appears from figure 6 in Williford and Maunsell (2006) that the additive gain model would perform at least as well as the other models tested in that study.

Our finding that the contrast-gain model gave the worst description of the effect of attention on contrast response functions implies that the effects of attention in area V1 are not equivalent to an increase in stimulus contrast, and do not support previous findings in area V4 (Reynolds et al., 2000) and area MT (Martinez-Trujillo and Treue, 2002). We found that the response-gain model also gave a poorer description of the data than the additive model. In contrast to the prediction of the response-gain model, the increase in the neuronal activity due to attention was not a constant proportion of the response. Instead, the attentional response modulation was already large for low to medium luminance contrast stimuli, especially in the curve tracing task where the responses of the majority of neurons were better described by the additive model. Another model that has been proposed previously is the so-called activity gain model that proposes that the spontaneous activity also increases if attention is directed to the RF. In contrast, we observed a significantly reduced level of ongoing activity with attention in the detection task, which is incompatible with the activity gain model. To our knowledge no other study has reported a reduction of ongoing activity with attention, although this could provide a mechanism to increase the signal-to-noise ratio and thereby aid in stimulus detection.

Previous studies have shown that task difficulty affects neuronal responses (Chen et al., 2008; Spitzer et al., 1988). In both tasks performance varied with stimulus contrast (albeit only in one of the monkeys in the detection task). This means that the task was more difficult for low contrast stimuli. If task difficulty had an influence on neuronal activity, we would expect the largest attentional modulations for low contrast stimuli, and less modulation for the high contrast stimuli. Such a scenario would predict that the contrast gain model would result in a better fit than either of the alternative models. Alternatively, it might increase the attentional modulation more strongly for low contrast stimuli than for high contrast stimuli. A combination of a response gain model and a task difficulty model would then either generate additive effects of attention on neuronal responses or result in a combined contrast/response gain model. However, this scenario would also suggest that the attentional effects are profound at the lowest contrasts (where the task is hardest), while we found little attentional modulation for the lowest contrast. Moreover, we found that a combined contrast/response gain model resulted in significantly larger normalized $\chi^2$ values than the additive model, and could thus be discounted. Finally, in monkey H (which performed the detection task) task difficulty did not vary with stimulus contrast, but we still found the same pattern of attentional
modulation, namely that the additive model explained our data best. From these results we infer that it is not simply a combination of multiplicative gain control with varying task difficulty that results in the superiority of the additive gain model.

**Contrast response functions in striate and extrastriate visual cortex**

The first studies of contrast sensitivity in area V1 were carried out in anaesthetized monkeys and reported median $c50$ values of 24% (Albrecht and Hamilton, 1982) and 33% (Sclar et al., 1992). In our study the $c50$ values generally fell between 11 and 17%, which is lower than in the anaesthetized animals but at the same time higher than the value of 7% that was recently reported by Palmer et al. (Palmer et al., 2007) in the awake monkey. An important difference between the present study and the one by Palmer et al. (Palmer et al., 2007) is that we used stimuli with a negative luminance contrast (i.e. with a higher background luminance). We have also tested the MUA-recording sites with bright curves on a dark background in the curve tracing task and obtained $c50$ values of 5-6% (data not shown), which implies that the contrast sensitivity of V1 neurons may depend on the contrast polarity.

Some of the V1 neurons had $c50$ values that were smaller than the $c50$ values of ~15% that have been reported for area V4 (Williford and Maunsell, 2006). This result is noteworthy as it suggests that pooling the activity across multiple V1 neurons either does not increase contrast sensitivity as is often thought (Sclar et al., 1992; Thiele et al., 2000; Williford and Maunsell, 2006), or that the contribution of area V4 to the detection of low contrast stimuli is limited.

**Strength of attentional modulation in area V1 and in higher areas**

We observed robust effects of attention on neuronal firing rates in area V1 in each of our 4 monkeys in two different tasks. These effects were small or absent during the initial transient response, but were profound during the sustained response period as has been observed previously in area V1 (Roberts et al., 2007; Roelfsema et al., 1998) and area V4 (Reynolds et al., 2000). We found that attention increased firing rates by ~10-20% at medium and high luminance contrast. These attentional effects on the strength of neuronal responses in area V1 are comparable to the effects that have been observed in area V4 (Williford and Maunsell, 2006) (see their Figure 6 E and H) or even larger (Reynolds et al., 2000) (their Figure 5A). Our results are therefore compatible with a study by Motter (Motter, 1993), who demonstrated that the effects of selective attention on the neuronal responses in area V1, V2 and V4 have a similar magnitude.

The magnitude of attentional modulation in area V1 is also similar to the strength of the effects of attention in areas MT and MST (Treue and Maunsell, 1999; Treue and Maunsell,
All these results, taken together, suggest that the magnitude of attentional effects remains relatively constant when ascending the cortical hierarchy up to the level of areas V4 and MT. The strength of attentional modulation may thus not be determined by the cortical hierarchy, but rather by the visual stimulus that requires attention (Roberts et al., 2007) and by how useful neuronal selectivity in an area is for the task at hand (Roelfsema and Spekreijse, 2001).

**Additive effects of attention**

To summarize, we observed that attention increases the neuronal response by a relatively constant amount once the stimulus has enough contrast to become visible. This finding agrees to some extent with a recent fMRI study in human observers showing that the effect of attention on the BOLD response in area V1 is relatively independent of stimulus contrast (Buracas and Boynton, 2007; Murray, 2008). However, there are also important differences. In our data the additive component only becomes active once the stimulus reaches detection threshold, while the fMRI data show significant effects on baseline responses, i.e. in the absence of a stimulus. Thus, the fMRI data, which measure BOLD activity might reflect a change in subthreshold membrane potential of V1 neurons, or even a predominant effect on blood supply when no stimulus is presented. Buracas and Boynton (2007) also reported that the effect of attention on the contrast response functions in areas V2 and V3 are equally well described by an additive model. In a yet higher visual area, area LOC, Murray & He (Murray and He, 2006) observed that the neuronal responses evoked by an attended stimulus are relatively invariant across variations in contrast, while the responses evoked by an unattended stimulus do not exhibit the same degree of contrast invariance. We suggest that the neurons that represent the attended stimulus in higher areas might feed back to earlier areas in a manner that is relatively independent of contrast. In this view, the extra activity in earlier areas due to the attentional feedback depends little on stimulus contrast once the stimulus has sufficient visibility to be registered in the higher visual areas.

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