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TASK DIFFICULTY MODULATES ACTIVITY OF SPECIFIC NEURONAL POPULATIONS IN PRIMARY VISUAL CORTEX

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Abstract

Spatial attention enhances our ability to detect stimuli at restricted regions of the visual field. This enhancement is thought to depend on the difficulty of the task being performed, but the underlying neuronal mechanisms for this dependency remain largely unknown. Here we demonstrate that task difficulty modulates neuronal firing rate at the earliest stages of cortical visual processing (area V1) in the macaque monkey. These modulations are spatially specific: increasing task difficulty enhances V1 neuronal firing rate at the focus of attention and suppresses it in regions surrounding the focus. Moreover, we show that response enhancement and suppression are mediated by distinct populations of neurons that differ in direction selectivity, spike width, interspike interval distribution and contrast sensitivity. Our results provide strong support for center-surround models of spatial attention and suggest that task difficulty modulates the activity of specific populations of neurons in the primary visual cortex.

An important function of our visual system is to detect rapid changes in the visual environment that could have behavioral significance. The speed^{1, 2} and sensitivity^{3, 4} of detection are improved by allocating selective attention to the regions of the visual field where the stimulus change is likely to occur. Moreover, increased task difficulty reduces the interference caused by peripheral distracters^{5, 6}, making the distracters more unlikely to deviate the focus of attention⁷.

While the behavioral benefits of spatial attention are well documented and its neuronal mechanisms are increasingly better understood^{8–12}, the role of task difficulty on attentional gain is still unclear. Task difficulty modulates fMRI BOLD signals at multiple stages of the visual pathway, including area V1^{13–15}. However, electrophysiological recordings have found task-difficulty modulated responses only in higher cortical areas such as area V4^{16, 17}, IT¹⁸ and the prefrontal cortex^{19, 20}. Moreover, whereas previous electrophysiological studies in area V4 indicated that the main effect of increasing task difficulty was an enhancement in visual responses¹⁶, a more recent study has found evidence for suppression of visual responses as well¹⁷.

Precise measurements of task-difficulty modulations throughout the cortical visual hierarchy are important to understanding the relative contribution of each area to attentional gain²¹.

While it is now widely accepted that spatial attention modulates the activity of neurons in area V1^{11, 22–27}, the extent that V1 activity is modulated by task difficulty remains unclear²⁸. Moreover, it is unknown what cell types are most strongly modulated as a function of task difficulty. For example, a recent study in area V4 indicates that both putative inhibitory and excitatory neurons are modulated by spatial attention²⁹, but it is not known if both cell types are modulated in earlier cortical areas such as area V1. Here, we used a technique that allowed us to study the visual responses of well-isolated V1 neurons with a great level of detail and to vary the difficulty of an attention task that was spatially localized either inside or outside the neuronal receptive fields. We found that task difficulty strongly modulates V1 activity and that these modulations can enhance or suppress V1 neuronal responses. Moreover, we demonstrate that the amount of suppression and enhancement depends on the receptive field location (relative to the focus of attention) and the functional properties of the V1 neurons. Some of these results were published in abstract form (Chen et al., *Soc. Neurosci. Abstr.* 286.14, 2005).

RESULTS

Well-isolated V1 neurons were recorded from two rhesus monkeys while performing a task that required fast detection of a visual stimulus. The recordings were obtained by using an implantable, multielectrode/microdrive array with ultra-thin electrodes³⁰ that allowed us to study each neuron for several hours. The recording stability combined with the excellent spike isolation allowed us to measure the response properties from each neuron with great level of detail (Supplementary Fig. 1). In addition to quantifying response modulations to spatial attention and task difficulty, we also measured orientation tuning, direction selectivity, spatial frequency tuning, receptive-field structure (by reverse correlation analysis), response latency, color selectivity, contrast sensitivity, spike width, interspike-interval distribution, response linearity (F1/F0) and spontaneous firing rate for each neuron. A main goal of this study was to characterize the functional properties of neurons that are modulated by spatial attention and task difficulty, so as to identify the specific types of neurons that mediate attentional effects.

Effects of spatial attention and task difficulty

During the recordings, monkeys held a bar and fixated a small cross while attending to one of five peripheral drifting gratings, which was cued at the beginning of each trial (Fig. 1a). The five gratings had different spatial locations but they were all identical in orientation and direction of movement, spatial frequency, temporal frequency and size (matching the response properties of the neuron studied). After a randomized period of time that lasted 1.5–3 seconds, the cued grating changed color and the monkey indicated the color change by releasing the bar as fast as possible (shorter reaction times resulted in larger rewards; reaction times longer than 500 ms were not rewarded). Response modulations to spatial attention and task difficulty were measured within the 500 ms preceding the color change (1–2.5 seconds after the cue was turned off, Fig. 1a, top). The color change could be either easy or hard to detect (due to the change in its color/luminance contrast) and it could take place either inside or outside of the neuron's receptive field (Fig. 1b, see Methods). The level of task difficulty was adjusted in each recording session to obtain reaction times that were significantly longer during the hard task than the easy task ($P < 0.05$ in Wilcoxon test). The cue was blocked for both spatial location and difficulty for 20 or more consecutive trials so that the monkeys could maximize their effort within a trial block (i.e. if the first trial was difficult to detect, the monkeys knew that the following trials would be also difficult and would need to increase their effort to maximize reward). We studied visual responses from 92 neurons at two or more different levels of task difficulty and two spatial locations of attention. We also measured in detail the response properties of each neuron (average recording duration: 1.6 hours; see Supplementary Fig. 1).

During the easy task, the monkeys detected the color change rapidly (average reaction time: 337 ± 47 ms) and made few mistakes (percentage of rewarded bar releases: 98%), but only 8 out of 92 V1 neurons (8%) were modulated by spatial attention (Fig. 1c, top; see methods for data on each monkey). During the hard task, the reaction times were significantly higher (394 ± 61 ms, $P < 0.0001$ Wilcoxon test), errors were more frequent (percentage of rewarded bar releases: 86%) and 39 out of 92 neurons in V1 (42%) were modulated by spatial attention (Fig. 1c, bottom; all cells modulated by attention during the easy task were also modulated during the hard task). We selected the cells that were significantly modulated by attention for further analysis ($n = 39$, red bars in Fig. 1c, $P < 0.05$ in Wilcoxon test, see Methods for measurements of significance). Throughout the text, visual responses measured in the four different conditions of task difficulty and spatial attention will be referred to as E (responses during the easy task), H (responses during the hard task), I (responses while the focus of attention was inside the receptive field) and O (responses while the focus of attention was outside the receptive field).

The modulation of V1 visual responses by spatial attention and task difficulty are illustrated with two representative cell examples in Figure 2. The top of the figure shows the peristimulus time histograms (PSTHs) of the visual responses driven by the last grating cycle before the color change (see Fig. 1a for details about the temporal course of stimulus and response). Each PSTH shows responses to different levels of difficulty (easy in blue, hard in red and intermediate in black) and different spatial locations of attention (left: attention inside the receptive field; right: attention outside the receptive field). The panels below the PSTHs illustrate different functional properties measured in each neuron (i.e. spike width, interspike interval distribution, receptive field, direction selectivity and spatial frequency tuning). As illustrated in this figure, the most pronounced effect of increasing task difficulty in cell_a (from an easy to a hard task) was response enhancement when spatial attention was located inside the receptive field. In contrast, the most pronounced effect of increasing task difficulty in cell_b was response suppression when attention was located outside the receptive field. Cell_a and cell_b differed in several other response properties. Cell_b had wider spike waveforms and a tighter interspike-interval distribution than cell_a. Moreover, unlike cell_a, cell_b was direction selective, color selective (not shown) and it could not be visually driven with sparse noise stimuli (light and dark spots presented for 40 ms within the receptive field). Other properties such as spatial frequency tuning and Fourier harmonic F1/F0 ratio were similar in both cells.

On average, the attentional ratio $[(I - O)/(I + O)]$ of attention-modulated V1-cells was 0.09 during the hard task, which corresponds to a mean response enhancement of 22% $[(I - O)/I * 100]$ when spatial attention was located inside versus outside the receptive field. In contrast, the average attentional ratio during the easy task was significantly lower, 0.03 ($P < 0.0001$ Wilcoxon test), which corresponds to a modest enhancement of just 7% when attention was inside versus outside the receptive field (Fig. 3a). Clearly, increasing task difficulty made the attentional modulations much stronger within area V1, from a 7% modulation, which matches some V1 measurements in previous studies²¹, to a 22% modulation, which approaches the modulations measured in higher cortical areas^{8, 10, 21}.

The effect of task difficulty on visual responses was spatially specific. Increasing task difficulty (from an easy to a hard task) enhanced the visual responses of cells with receptive fields at the focus of attention and suppressed the responses of cells with receptive fields outside the focus. We measured the difficulty ratio $[(H - E)/(H + E)]$ of the responses from the attention-modulated cells at two spatial locations of attention (Fig. 3b). When spatial attention was inside the receptive field, most difficulty ratios were positive (30 out of 39, $P = 0.0008$, Chi-square test) indicating that V1 neurons responded more strongly during the hard task than the easy task (response enhancement). In contrast, when spatial attention was located outside the receptive field, most difficulty ratios were negative (28 out of 39, $P = 0.006$, Chi-square test)

indicating that V1 neurons responded less strongly during the hard task than the easy task (response suppression). The magnitudes of the response enhancement and response suppression were significantly correlated to each other ($r = 0.56$, $P < 0.001$, Fig. 3c). That is, neurons that showed the strongest response suppression when spatial attention was outside the receptive field showed the weakest response enhancement when spatial attention was inside the receptive field. Conversely, neurons that showed the strongest response enhancement when attention was inside the receptive field showed no response suppression when attention was outside the receptive field. This suggests that the response suppression and response enhancement driven by an increase in task difficulty could be mediated by different populations of neurons. We investigated this idea further by performing a detailed study of the functional properties of neurons modulated by attention.

Functional properties of V1 neurons

Intrigued by the differences in the response properties of cell_a and cell_b, we divided our population of attentionally modulated cells into two groups: difficulty-enhanced and difficulty-suppressed neurons. We called difficulty-enhanced neurons those cells that showed a net enhancement in visual response with task difficulty, such as cell_a ($n = 20$) and difficulty-suppressed neurons those that showed a net suppression of visual responses, such as cell_b ($n = 19$). By definition, difficulty-enhanced neurons generate the strongest visual responses when the task is hard (Fig. 4a, left) and difficulty-suppressed neurons generate the strongest visual responses when the task is easy (Fig. 4b, left). We noticed that difficulty-enhanced neurons, such as cell_a, were usually non-directional selective, had narrow spike-widths and broad interspike interval distributions, as illustrated by four cell examples in Figure 4a (middle and right). In contrast, difficulty-suppressed neurons, such as cell_b, were directional selective, had broader spike-widths and tighter interspike interval distributions (Fig. 4b, middle and right).

To quantify the relation between task-difficulty modulations and neuronal functional properties, we calculated a summed difficulty ratio for each cell as $(H_s - E_s)/(H_s + E_s)$, where $H_s = IH + OH$ and $E_s = IE + OE$. A positive ratio indicates that the cell responded more strongly during the hard task than the easy task (independently of the location of attention) and a negative ratio indicates that the cell responded more strongly during the easy task. Consistent with the examples shown above, the summed difficulty ratio was correlated with the cell direction selectivity both in the sample of cells modulated by spatial attention ($r = -0.58$, $P < 0.001$, $n = 39$, Fig. 5a) and in the entire sample ($r = -0.25$, $P < 0.02$, $n = 92$, not shown). Moreover, the summed difficulty ratio was correlated with the cell's spike width ($r = -0.58$, $P < 0.001$, Fig. 5b), and the peak of the interspike-interval distribution ($r = 0.45$, $P < 0.004$, Fig. 5c). We also found a correlation between the summed difficulty ratio and contrast sensitivity ($r = 0.51$, $P < 0.03$) although the sample of cells tested for contrast was smaller ($n = 19$; Fig. 5d). Interestingly, the regression lines from some of these correlations seemed to link two separate clusters of cells rather than a continuum (Fig. 5a).

To estimate the significance of this observation, all the scatter plots from Figure 5 were tested for bimodality³¹ (Hartigan tests were run in histograms with X-axes parallel to the regression lines). These tests revealed a significant bimodal distribution in the projection defined by direction selectivity and the summed-difficulty-ratio (Fig. 5a, $P = 0.018$), supporting the notion that difficulty-enhanced and difficulty-suppressed neurons form two separate clusters. Interestingly, neurons whose responses were not modulated by spatial attention had intermediate properties between these two clusters (Fig. 6 and Table 1). Other response properties were also compared between clusters but were not significantly different. These included mean firing rate, response linearity (F1/F0 ratio), color sensitivity, spatial frequency

tuning (peak and bandwidth), orientation tuning (circular variance), receptive field size, response latency and visual responses to brief dark/light spots (Supplementary Fig. 2).

Ideally, the attentional modulations should be measured at multiple levels of task difficulty to quantify the correlation between task difficulty and response magnitude. However, it was not technically possible to measure multiple levels of task difficulty and acquire detailed quantification of the response properties from each cell, due primarily to the amount of time that the animals were willing to work. To address this limitation, in a group of cells ($n = 59$) we gave priority to the measurement of attentional modulations over response properties and studied three or more levels of difficulty at two spatial locations. Within 22 attention-modulated cells in the group, seven of them were classified as difficulty-enhanced (summed difficulty ratio > 0) and six as difficulty-suppressed (summed difficulty ratio < 0). We calculated separate correlation coefficients for difficulty-enhanced and difficulty-suppressed neurons by measuring the mean firing rate at three different levels of difficulty (hard, medium and easy) and then normalizing the mean firing rate after dividing by the maximum mean rate obtained under the three conditions. Consistent with the results reported above, the mean firing rate of the difficulty-enhanced neurons was positively correlated with task difficulty only when the spatial attention was inside of the receptive field (attention inside the receptive field: $r = 0.66$, $P < 0.0001$; attention outside the receptive field: $r = 0.07$, $P = 0.69$). In contrast, the mean firing rate of the difficulty-suppressed neurons was correlated with attention difficulty only when attention was outside of the receptive field (attention inside the receptive field: $r = 0.12$, $P = 0.55$; attention outside the receptive field ($r = -0.77$, $P < 0.0001$; Fig. 7).

Discussion

Our results demonstrate that task difficulty modulates the activity of single neurons within the primary visual cortex and that attentional gain can be enhanced by a factor of about 3 when task difficulty is increased (Fig. 3a). We show that the increase in V1 attentional gain is obtained through a center-surround mechanism that enhances visual responses at the focus of attention and suppresses visual responses outside the focus (Fig. 3b). We also demonstrate that the amount of response enhancement and suppression are correlated across neurons: neurons that show the strongest suppression when attention is outside the receptive field show the weakest response enhancement when attention is inside the receptive field, and vice versa (Fig. 3c).

Finally, we show that response enhancements and suppressions are mediated by two distinct populations of neurons with different response properties (Fig. 5 and Table 1). The difficulty-suppressed neurons are more directionally selective, have tighter interspike interval distributions, wider spikes and higher contrast sensitivity than the difficulty-enhanced neurons. These two populations of neurons may work together to increase sensitivity at the focus of attention while suppressing distractions caused by peripheral transient movement⁷. Also, there may be laminar differences corresponding to the two populations of neurons modulated by attention. It is interesting to note that some functional properties of difficulty-suppressed neurons (i.e. high directional selectivity and high contrast sensitivity) match the functional properties of V1 neurons projecting to area MT³³. This match is interesting because area MT is involved in detecting fast transient movement that could lead to shifts in the spatial focus of attention^{34, 35}.

Task-difficulty modulations in visual cortex

Human psychophysical studies have demonstrated that visual detection is strongly dependent on the location of spatial attention^{1, 3} and that increasing task difficulty significantly reduces the amount of interference caused by peripheral distracters^{5, 6}. However, the neuronal mechanisms responsible for the reduction in peripheral interference are not well understood. The first measurements of task-difficulty modulations at the level of single neurons were

performed in area V4 and revealed an increase in visual responses with task difficulty¹⁶. More recent measurements in the same area found evidence also for response suppression¹⁷. The response suppression described in area V4 provided a neuronal mechanism for a reduction of peripheral interference during high attentional load. However, it remained unclear whether this suppressive mechanism (at the level of single cells) was restricted to high cortical areas or could be found at earlier stages of cortical processing.

Previous electrophysiological measurements using chronically-implanted micro-wires and recordings from multiunit activity did not find evidence for task-difficulty modulations in area V1²⁸. However, whereas recordings from multiunit activity³⁶ (and local field potentials³⁷) are a powerful approach to measure the average attentional modulation across clusters of neurons, they could easily miss modulations restricted to specific cell types. On the other hand, there is evidence from fMRI in humans that V1 signals are modulated by task difficulty^{13–15, 38, 39} and the findings reported here provide a correlate at the level of primate single neurons for these fMRI measurements.

Potential contribution of small eye movements

Although our results clearly demonstrate the existence of task-difficulty modulations in area V1, a potential contribution from small microsaccade movements to these modulations must be carefully evaluated. Microsaccades increase the firing rate of V1 neurons during fixation^{40, 41}, therefore, differences in microsaccade frequency could potentially generate different firing rates in the various conditions tested here.

There are several reasons why microsaccades are unlikely to affect our measurements. First, microsaccade frequency was not significantly different between the easy and hard task (0.40 ± 0.02 Hz versus 0.45 ± 0.02 Hz, $P = 0.087$, Wilcoxon test). Second, the average eye position and fixation stability were similar across conditions and were not correlated with either the location of attention or the task difficulty (see Supplementary Fig. 3). Third, our results could be replicated when we selected trials without microsaccades (see methods). And finally, it would be difficult to explain how a small change in microsaccade frequency or eye position could generate the correlations reported here between the magnitude of the visual response and the cell's response properties (Fig. 5). For the eye movements to generate these correlations, the monkeys would have to be aware of the direction selectivity of the cell recorded and the location of the neuronal receptive field and use this information to generate patterns of eye movements that consistently suppressed the response of directional cells only when paying attention outside of the receptive field.

Selective spatial attention during the easy task

It is important to emphasize that the monkeys had to attend selectively even when performing the easy task. For example, if the color change was very noticeable, the monkeys could detect it as a bottom-up pre-attentional 'pop-out' effect instead of as a result of top-down selective spatial attention. This scenario is unlikely for several reasons. First, the color change was subtle (see methods) and monkeys reacted significantly faster when the spatial location of the change was cued at the beginning of the trial (see methods for detail). Second, at the end of most trials the monkeys made saccades aimed at the cued spatial location, indicating that they were paying attention to this region of visual space (Supplementary Fig. 4). Third, we found strong spatially-selective correlations between the level of task difficulty and the magnitude of the visual response (Fig. 7; since these correlations required the use of at least three levels of difficulty, it is clear that the monkeys used spatial attention to perform tasks that differed in difficulty). Fourth, a main result from this study (the correlation between difficulty-modulations and direction selectivity) could be replicated in a foveal task, in which the monkey must pay attention always, independently of task difficulty (see Supplementary Fig. 5 for details).

Finally, the task was designed to highly reward increased effort: the faster the detection the larger the reward. Since monkeys are primarily motivated to perform for the reward, it is unlikely that they would increase the attentional effort during the hard task and at the same time failed to pay attention during the easy task, which is when they could best hope to achieve maximal reward.

Neuronal circuitry of visual attention

Our results suggest that the neuronal network of visual spatial attention involves not only specific brain areas ^{8, 12, 21} but also specific neuronal populations within each area. It is interesting to speculate that the attention-enhanced neurons with short-duration spikes may have been fast-spiking GABAergic interneurons. This conclusion is consistent with a recent study in area V4 that found strong attentional modulations in neurons with different spike widths ²⁹ (the distribution of spike widths in our sample of V1 neurons shares certain resemblance with the distribution reported by Mitchell et al. in area V4, Supplementary Fig. 6).

The finding that task difficulty can enhance or suppress visual responses within area V1 has important implications for current models of spatial attention. Whereas response enhancement could be explained by a spotlight that ‘increases in intensity’ with attentional load, the response suppression is better explained by models that emphasize the role of response-suppression and center-surround interactions in spatial attention ^{8, 10, 22, 24, 42–47}. Most mathematical models of visual attention assume that response suppression is mediated by intracortical inhibition ^{10, 44}. Our results support these models by showing that neurons with the thinnest spikes (putative inhibitory neurons) enhanced their visual responses with increased task-difficulty, whereas neurons with the broadest spikes (unlikely to be inhibitory neurons) suppressed their responses (Supplementary Fig. 6). Consistent with these models ^{10, 44}, our results also indicate that the strongest inhibition should be found inside the focus of attention since the difficulty-enhanced neurons increased their responses more strongly when the focus of attention was inside the receptive field (Fig. 3c). It is important to note, however, that not all inhibitory populations have short-duration spikes and, conversely, that some cortical spiny neurons have very brief spikes ⁴⁸.

An important finding of this study is that difficulty-suppressed neurons are more directional selective and have tighter interspike interval-distributions (i.e. more transient responses) than difficulty-enhanced neurons. Moreover, although neurons with the thinnest spikes are all difficulty-enhanced, neurons with broad spikes (presumably excitatory neurons) can be either difficulty-enhanced or difficulty-suppressed (Supplementary Fig. 6). Based on this finding, we would like to propose a conceptual model for the V1 neuronal circuitry involved in visual attention (Supplementary Fig. 7). According to this model, an increase in attentional load has two different effects on V1 neuronal responses. First, it increases the visual responses of non-directional/sustained neurons at the focus of attention to improve detection. Second, it reduces the neuronal responses of directional/transient cells outside the focus of attention to suppress distraction. We speculate that neurons with enhanced responses are part of a neuronal network involved in making detection more reliable at the focus of attention. And neurons with suppressed responses are part of a neuronal network involved in detecting transient movement in the visual periphery, which needs to be suppressed to avoid attentional shifts during difficult detection tasks. As part of this conceptual model, we predict that, unlike V4 cells ^{16, 17}, most V1 neurons projecting to area MT (and perhaps most MT neurons) should be difficulty-suppressed.

Taken together with results from previous studies ^{16, 17}, our findings suggest that the mechanisms driving task difficulty modulations of neuronal responses are likely to be similar in both early and late cortical stages of visual processing. Moreover, our study provides further

evidence that area V1 plays an important role in the neural network of visual attention^{11, 22–24, 49, 50}.

METHODS

Surgical procedures

Experiments were performed in two adult rhesus monkeys (*Macaca Mulatta*). Surgery was performed under general anesthesia and sterile conditions in a surgical suite (see supplementary methods for detail). Each macaque was implanted with a head post for head stabilization, a scleral eye coil to monitor visual fixation and a recording chamber. The recording chamber contained arrays of 3–5 independently movable electrodes³⁰ that remained implanted in the brain for 6 months to >1 year (some of the electrodes were changed without removing the implant). During this time, the interior of the recording chamber remained sealed. The electrodes were made of a platinum-alloy core (platinum 90%, tungsten 10%) with a quartz coating, both of which are very durable and stable materials when chronically implanted in the brain³⁰ (see also Chen et al., *Soc. Neurosci. Abstr.* 286.14, 2005). They had a maximum shaft diameter of 40 microns and were pulled to a taper and sharpened to a fine tip. The short length of the electrodes and their attachment to the skull resulted in excellent recording stability, allowing us to study well-isolated neurons for long periods of time (Supplementary Fig. 1). During the electrophysiological recordings the animals had controlled water access and obtained most of their fluid intake (water or juice) by performing the behavioral tasks during the experiment. All the animal procedures were approved by the Institutional Animal Care and Use Committee (IACUC) at the State University of New York, College of Optometry and followed the recommendations of the NIH Guide for the Care and Use of Laboratory Animals and the Animal Welfare Act of 1986 and its revisions.

Behavioral task

Response modulations by spatial attention and task difficulty were measured while the macaques performed a behavioural task. A small fixation cross and a thin red ring were presented after the animal grabbed a bar. The ring had a diameter 3 times larger than the diameter of the neuronal receptive field, it was presented for 500 ms and served as a cue to indicate the spatial location to be attended. This thin ring was separated by 1–2.5 seconds from the time window used to measure response modulations by attention/difficulty. After the ring disappeared, 5 gratings were presented at 5 different locations. Following a randomized period of time (1.5–3 seconds) the grating at the cued spatial location changed color and the animal was tasked with releasing the bar as fast as possible to obtain a reward.

The cued grating could be the one located inside the receptive field or one of the other 4 gratings located outside of the receptive field. The color change could be either very noticeable (easy task) or difficult to detect (hard task). The cued grating was kept at the same spatial location for at least 20 trials so that the monkeys could adjust their effort to maximize reward. The two spatial locations of the cued grating (inside or outside the receptive field) were equidistant from the point of fixation and were separated from each other by 14° to 22°. Once the grating changed color, the primate had 500 ms to release the bar and receive a reward.

The amount of reward was determined by the reaction time according to the following linear equation:

$$R = -0.02 \cdot RT + 12$$

where R is the reward (number of juice drops) and RT is the reaction time. Because reaction times longer than 500 ms were not rewarded, the animal had to make a greater effort during the hard task than the easy task to obtain large rewards. The color/luminance change was

adjusted at each recording session until the reaction times during the hard task and easy task were significantly different.

The color/luminance was changed always at the trough of the grating (the luminance at peak of the grating remained constant at 109 cd/m²). The changes in color at the trough of the grating were very subtle and the amount of change depended on eccentricity, grating size, training experience and day-to-day variability. The value of the red gun ranged between 20%–52% for the hard task and 25%–67% for the easy task, which corresponds to a change in luminance of 1%–24% for the hard task and 8%–38% for the easy task.

Behavioral performance

The reaction times were significantly faster during the easy task (mean: 337 ms, median: 329 ms, range = 231–464 ms) than the hard task (mean: 376 ms, median: 394 ms, range: 278–500 ms; $P < 0.0001$ Wilcoxon test). In some experiments, we cued a spatial location that was different from the location where the grating changed color (10% of wrongly cued trials). In these experiments, the reaction times were 34 ms slower in the wrongly cued trials than in the trials that were cued correctly ($P < 0.0001$, Wilcoxon test) indicating that the animals were paying attention to the cued spatial location, where the color change had to be detected.

The reaction times for each monkey were as follows. For monkey Smitty the average reaction time was 328 ms during the easy task and 348 ms during the hard task ($P < 0.0001$, Wilcoxon test). For monkey Red, the average reaction time was 338 ms during the easy task and 403 ms during the hard task ($P < 0.0001$, Wilcoxon test). These reaction times were very short and the animals were highly motivated to obtain the largest reward possible both during the easy and hard tasks. Three naïve human subjects performing the easy task had all longer reaction times (JJ: 404 ms, CW: 421 ms, YW: 429 ms) than Smitty (328 ms) and Red (338 ms) even after being given specific instructions to pay attention to the location of the target and to make all possible efforts to be faster than the monkeys. The reaction times of two of the authors from this paper were also measured. One of us was faster than either monkey (YC: 318 ms) and the other slower (JMA: 434 ms).

Errors due to slow reaction time (the animal released the bar too late) were less frequent during the easy task (2%) than the hard task (average: 14%). The error rates for each monkey were as follows. Monkey Smitty made 1% of errors during the easy task and 8% of errors during the hard task. Monkey Red made 2% of errors during the easy task and 14% of errors during the hard task. Increasing the task difficulty also led to an increase in other types of errors that were not directly related to the color change, as if the animals were becoming more impatient with the difficult task. For example, both monkeys broke fixation more frequently during the hard task than the easy task (note that these breaks in fixation are probably a consequence of impatience and not fixation stability since the fixation stability was similar across conditions in non-aborted trials (Supplementary Fig. 4)). Monkey Red made significantly more early-release errors (i.e. bar released before the color change) during the hard task than the easy task ($P < 0.0001$, Wilcoxon test).

In total, we recorded from 214 V1 cells (108 in Smitty and 106 in Red). From this sample, 114 cells were studied with enough detail to be included in this paper. 92 cells were studied under different conditions of attention and task difficulty (15 in Smitty and 77 in Red) and 34 cells were studied foveally under different levels of detection difficulty (all in Smitty). The two monkeys (Smitty vs. Red) did not differ in the percentage of attentionally modulated cells (40% vs. 43%), difficulty ratios when attention was inside (0.0376 vs. 0.0316, $P = 0.4835$, Mann-Whitney test) or outside the receptive field (−0.101 vs. −0.0211, $P = 0.0114$, Mann-Whitney test) and attentional ratios during the easy task (−0.0037 vs. 0.0334, $P = 0.1391$, Mann-Whitney test). There was a significant difference in the attention ratios during the hard task (0.1349 vs.

0.0858, $P = 0.0091$, Mann-Whitney test) probably because task difficulty was increased more aggressively in the second monkey (Red). In the second monkey, we learned that we could make the task harder if we intercalated the easy task when the monkey started failing too frequently.

Data analysis and statistical analysis

The effects of spatial attention and task difficulty on visual responses were quantified as follows. First, we calculated the peristimulus time histogram (PSTH) of the visual response preceding the color change (500 ms time window, bin = 10 ms; the last cycle of the drifting grating, Fig. 1). Then, we fit this PSTH with a Gaussian function and obtained the time values (t_1 and t_2) at which the Gaussian was at half of its maximum amplitude. The average of the PSTH bins contained within this time window (t_1 and t_2) was used as a measurement of the visual response obtained under each level of task difficulty and spatial attention.

On average, we used twenty 10-msec bins around the PSTH peak to measure the attentional modulations (median: 18 bins). This statistical criterion was quite strict and reduced considerably the number of cells that were significantly modulated by attention (particularly during the easy task). However, the mean attentional and difficulty ratios were relatively independent of the time window used for the measurements (Supplementary Fig. 8). Only when the time window was narrowed down to one 10-msec bin, the measurements became very variable and the average differences lost statistical significance. We believe that the time window used here (half-width and half-height of the PSTH) is the most appropriate measurement for this study since the PSTH width varied across cells.

All the time windows selected for measurements of response modulation were separated by at least 1 second from the cue. The magnitude of the attentional ratios did not seem to depend on the duration of the time interval between cue and target. In the hard task, the strongest attentional ratio was obtained with delays of 2 seconds and the weakest with delays of 3 seconds, however, the difference was not significant (0.1 versus 0.07, $P = 0.18$, Mann-Whitney test). It should be noted that the monkeys made more errors in the longest trials (3 seconds) probably because they became impatient while waiting for the target (3 seconds was the maximum time duration that they accepted to perform this task).

The frequency of microsaccades was calculated using a method described in a previous study⁴¹. First, we plotted the vertical and horizontal eye movement recordings from 800 ms to 0 ms before the grating changed color and we created a table of change (dx and dy) for each trial, computed as the difference between successive 1-ms intervals. Then, we smoothed the differential values with a 31 ms-wide boxcar filter and converted the dx/dy values to polar coordinates, which represented the instantaneous direction (θ) and amplitude of the microsaccade (r). The number of microsaccades was estimated as the r -values that exceeded a threshold of 3 arcmin. The frequency of microsaccades was obtained by averaging the number of microsaccades across 800 ms trials.

We measured possible differences in eye position and fixation stability across testing conditions and cell types. We used four different time windows (800, 400, 200, 100 ms) and found no significant differences in the average eye position in > 76% of cases tested including all multiple conditions and multiple time windows (Wilcoxon test). In a minority of the cases, we did find statistically significant differences, but these differences were too small ($\leq 0.25^\circ$) to be a concern. In fact, if we had removed these cases from our sample, the main conclusions would stay the same. Moreover, these small offsets in eye position were not correlated with the location of attention and/or task difficulty indicating that they were most likely produced by a small drift in the eye coil measurements rather than a real drift in eye position. The distributions of differences in fixation position and fixation stability did not differ across

conditions and cell types (Supplementary Fig. 3). The size of the attentional effect was not correlated with the eccentricity of the cell recorded ($r = -0.06$, $P = 0.7$, mean attentional ratio was 0.09 both at < 10 deg and 10–20 deg). Finally, our main results could be replicated when the measurements were performed in selected trials without microsaccades. Similarly to the results reported in Figure 3, in the selected trials without microsaccades the mean attentional ratio was 0.09 for the hard task and 0.04 for the easy task; the mean difficulty ratio was 0.03 for attention inside of the receptive field and -0.03 for attention outside of the receptive field; and the response changes inside and outside of the receptive field were correlated ($r = 0.49$, $P < 0.002$).

Significant differences throughout the paper were assessed with a Wilcoxon test when comparing visual responses from the same cell or behavioural parameter (e.g. Fig. 3) and a Mann-Whitney test when comparing the response properties of different cells (e.g. Table 1).

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Figure 1. Behavioral task and attentional response ratios measured in V1 single cells during hard and easy tasks

(a) Temporal structure of a trial. Two rhesus monkeys were trained to fixate a small cross while covertly attending to a spatial location that was cued at the beginning of each trial. The cue was a thin red ring with a diameter 3 times larger than the diameter of the neuronal receptive field (RF). Following the cue, drifting gratings were presented simultaneously at 5 different spatial locations for 1.5–3 seconds. Following a randomized period of time, one of the gratings changed color/luminance and the animal was tasked with detecting the change by releasing a bar within 0.5 seconds. The attentional modulations were measured at the last cycle of the drifting grating before the color change. **(b)** The color change could be easy or hard to detect, and could occur inside or outside the receptive field. **(c)** The number of cells that were significantly modulated by attention (shown in red) was much lower during the easy task (top) than during the hard task (bottom). Eight cells were significantly modulated by attention during both the easy and the hard task.

Figure 2. Examples of two V1 cells whose responses were modulated by task difficulty and spatial attention

(a) Cell showing response enhancement with increasing task difficulty. The response enhancement was stronger when spatial attention was located inside the receptive field (left) as opposed to outside (right). The peristimulus time histograms (PSTHs) show visual responses 500 ms before the grating changed color (the last cycle of the drifting grating). The bar graphs on the top right corner of the PSTHs show the average firing rate and standard error (s.e.m.) measured from the PSTHs. The standard error is defined as one standard deviation divided by the square root of the sample size. The star indicates $P < 0.05$, Wilcoxon test. This cell was tested with three different levels of difficulty. The region below the PSTHs shows the spike

waveforms, ISI (interspike interval distribution obtained with drifting gratings), receptive field measured with reverse correlation, orientation tuning and spatial frequency tuning. **(b)** Cell showing strong response suppression with increasing task difficulty. When spatial attention was outside the receptive field, the cell response was significantly stronger during the easy task than the hard task (66 versus 45 spikes per s, $P = 0.009$, Wilcoxon test). Notice than during the easy task, this cell seemed to respond more strongly when attention was outside versus inside the receptive field, however, the difference was not significant (61 versus 66 spikes per s, $P = 0.57$, Wilcoxon test).

Figure 3. Spatial attention and task difficulty modulations of V1 visual responses

(a) The attentional ratio (AR) was independently calculated for the hard task (x axis) and easy task (y axis) as $AR = (I - O) / (I + O)$, where I is the visual response when spatial attention was inside the receptive field (RF) and O the visual response when spatial attention was outside the receptive field. During the easy task, some cells (including cell in Fig. 2b) had negative attentional ratios indicating stronger responses when attention was located outside versus inside the receptive field, however, all attentional ratios were positive during the hard task. The arrows indicate the average ratio and standard error (s.e.m.) for each condition. (b) Difficulty ratio (DR) calculated independently when spatial attention was inside or outside the receptive field as $DR = (H - E) / (H + E)$, where H is the visual response during the hard task and E is the visual response during the easy task. (c) Response change (RC) with increasing task difficulty, calculated independently when spatial attention was inside and outside the receptive field as $RC = (H - E) / E$. There was a positive correlation between the RC measured when spatial attention was inside and outside the receptive field. Open circles in the three plots (a, b, c) mark the cells illustrated in Figure 2 (the neuron illustrated in Fig. 2b has the lower Y-axis values in the three plots).

Figure 4. Modulation by task difficulty in V1 cells

The graphs on the left show normalized visual responses summed across the two spatial locations of attention, for the easy task (Easy I + O) and the hard task (Hard I + O). This graph includes all cells that were significantly modulated by spatial attention as defined in Fig. 1c. The graphs on the middle and right show the direction selectivity, spike width and interspike interval distribution of eight cells chosen as representative examples (including the cells illustrated in Fig. 2). **(a)** Cells that enhanced visual responses when task difficulty was increased. **(b)** Cells that suppressed visual responses when task difficulty was increased.

Figure 5. Response modulations to spatial attention and task difficulty are correlated with the direction selectivity, spike width, interspike interval and contrast sensitivity of the cell
A summed difficulty ratio (DRs) was calculated as $(Hs - Es) / (Hs + Es)$, where Hs is the visual response during the hard task and Es the visual response during the easy task (summed across I and O conditions). **(a)** Negative correlation between DRs and direction selectivity. **(b)** Negative correlation between DRs and spike width. **(c)** Positive correlation between DRs and the peak of the interspike interval distribution (ISI peak). **(d)** Positive correlation between DRs and the stimulus contrast that generated 50% of the maximum response (C_{50}). The spike width was measured from the beginning of the first phase of the spike waveform to the peak of the second phase. The ISI peak was measured as the ISI interval at the peak of ISI distribution obtained with drifting gratings (with a bin width of 1 ms). Blue and red circles illustrate difficulty-suppressed neurons and difficulty-enhanced neurons respectively.

Figure 6. Response properties that distinguish V1 cells classified as difficulty-suppressed (summed difficulty ratio < 0), difficulty-enhanced (summed difficulty ratio > 0) and non-modulated (no significant modulation by spatial attention as defined in Fig. 1c)

. Bar graphs represent the average direction selectivity (a), spike width (b), ISI peak (c), ISI width (d), spontaneous activity (e) and contrast at half-maximum response (C_{50}) (f) for each cell group. Standard errors are defined as in Figure 2. ***, $P < 0.001$; **, $P < 0.005$; *, $P < 0.05$; ns, not significant (Mann-Whitney test).

Figure 7. The magnitude of the visual responses was correlated with the level of task difficulty (a) Normalized firing rate of difficulty-enhanced neurons measured at different levels of difficulty when attention was inside (left) and outside (right) the receptive field. The visual responses of the difficulty-enhanced neurons were positively correlated with task difficulty only when attention was located inside the receptive field ($r = 0.69$, $P < 0.0001$). (b) Normalized firing rate of difficulty-suppressed neurons. The visual responses of difficulty-suppressed neurons were negatively correlated with task difficulty only when spatial attention was located outside the receptive field ($r = -0.82$, $P < 0.0001$).

Table 1**Functional differences between two populations of V1 neurons, difficulty-suppressed and difficulty-enhanced**

The width of the interspike interval distribution was measured at half of its amplitude and the peak as the time with the maximum value in the distribution (measured with a bin width = 1 ms). The contrast sensitivity was measured from the contrast response function as the contrast that generated half-maximum response or C_{50} . Significance was measured with a Mann-Whitney test

Two types of V1 neurons modulated by spatial attention			
	Suppressed	Enhanced	Significance
$(H_{I+O} - E_{I+O})/(H_{I+O} + E_{I+O})$	-0.03	0.03	$P < 0.0001$
$ IH - IE / OH - OE $	0.42	5.48	$P < 0.0001$
Directional index	0.74	0.24	$P < 0.0001$
Spike width (μ s)	418	313	$P < 0.0001$
ISI peak (ms)	3.3	6	$P < 0.005$
ISI width (ms)	4.8	10.6	$P < 0.0001$
Contrast at half max. resp.	9.6	34.3	$P = 0.003$