Attention to Both Space and Feature Modulates Neuronal Responses in Macaque Area V4

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McAdams, Carrie J. and John H. R. Maunsell. Attention to both space and feature modulates neuronal responses in macaque area V4. *J. Neurophysiol.* 83: 1751–1755, 2000. Attention is the mechanism with which we select specific aspects of our environment for processing. Psychological experiments have shown that attention can be directed to a spatial location or to a particular object. Electrophysiological studies in trained macaque monkeys have found that attention can strengthen the responses of neurons in cortical area V4. Some of these studies have attributed these effects to spatial attention, whereas others have suggested that feature-directed attention may modulate the neuronal response. Here we report that neuronal correlates for both spatial and feature-directed attention exist in individual neurons in area V4 of behaving rhesus monkeys.

INTRODUCTION

Attention can be directed at different attributes of the environment. We can perform many tasks which seem to require different types of stimulus processing. Clearly, catching a flying object and determining what object is flying are different tasks. Catching the object requires computations of its velocity and trajectory. Determining the identity of the object requires a comparison of the visual attributes of the object with the attributes of other stimuli.

Experiments examining reaction times in human subjects suggest that attention may be directed to either or both stimulus location or feature. Maljkovic and Nakayama (1994, 1996) examined reaction times in pop-out tasks. They found that reaction times decreased when either the feature that defined the target or the location of the target was the same on consecutive trials. Additionally, the improvements in reaction time showed summation, suggesting that feature and position may use different attentional mechanisms. Baylis and Driver (1992) demonstrated that the ability of distractors to interfere with recognition of the target depends on both the spatial proximity of the distractors to the target and whether the target and distractor are the same color. They suggested that attentional allocation depends on the similarity of the target and distractors, because the visual scene is parsed according to Gestalt principles of perceptual organization.

Neuronal correlates of attention have also been measured in many different cortical areas using electrophysiological recordings from single neurons in behaving monkeys. Neurons throughout extrastriate visual cortex show increased responses when the animal's attention is directed to stimuli that are in the receptive field of the neuron being recorded (Bushnell et al. 1981; Connor et al. 1996, 1997; Mountcastle et al. 1987; Sato 1988; Treue and Maunsell 1996). Increased neuronal responses have also been found when attention is allocated on the basis of stimulus feature (Haenny et al. 1988; Maunsell et al. 1991; Motter 1994a,b). However two important issues remain. Is the neuronal input that results in a modulation in a spatial attention task different from the input that causes modulation in a feature-directed attention task? Are the same neurons involved in performing both spatial and feature-directed attention tasks?

METHODS

All experimental procedures and care of the animals were carried out in compliance with guidelines established by the National Institutes of Health.

Behavioral paradigms

We examined the effects of attention by recording from neurons in monkeys while they performed a task that required them to shift their attention to stimuli at different locations in visual field. Data were collected from two male rhesus monkeys (*Macaca mulatta*). Water intake was controlled and each animal was trained to perform a behavioral task using operant conditioning with a juice reward. Partway through training, an aseptic surgery was performed to implant a head post and scleral search coil (Judge et al. 1980). The animal was required to fixate within 0.7° of a fixation point throughout each trial using the scleral search coil to monitor eye position (Robinson 1963). Eye positions were analyzed to ensure that differences in the neuronal responses could not be attributed to differences in fixation position. The median fixation difference for the two tasks for both animals was <0.10°.

The monkeys were trained to do a delayed match-to-sample task with two versions (Fig. 1). In both versions, visual stimuli were presented at two locations on each trial: one inside the receptive field of the neuron being recorded from and one outside that neuron's receptive field. The animal was required to report whether the sample and test stimuli shown at one location were the same or different. In the spatial attention task, the visual stimuli at both locations were Gabor stimuli (Space, Fig. 1A). The animal's task was to report whether the orientation of the sample and test at one location were the same. In one mode, attended, the animal had to report on the stimuli inside the receptive field of the neuron being recorded. In the other mode, unattended, the animal had to report on the stimuli outside that neuron's receptive field. This task variant was called the spatial attention task because the neuronal correlate for attention that we were measuring depended on the difference between the animal attending to equivalent stimuli at different locations.

Another task involved both spatial and feature-directed attention (Space and Feature, Fig. 1*B*). In this task, the visual stimuli in the receptive field were again Gabors, but those outside the receptive field were isoluminant, colored, 2-D Gaussians. As in the spatial task in the

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FIG. 1. Behavioral tasks. Each frame represents different phases of a trial, with the fixation spot in the center and the neuron's receptive field indicated by a dashed oval. For both tasks, the monkey was required to hold his gaze on the fixation point and to depress a lever to begin the trial. In the spatial attention task (Space, *A*), both stimuli were Gabors. In the space-and-feature attention task (Space and Feature, *B*), the stimuli in the receptive field were Gabors and the stimuli outside the receptive field were colored, 2-D Gaussian patches. In attended modes, the monkey had to pay attention to the stimuli outside the receptive field. Fix, sample, and delay periods were 500 ms; the test period lasted either until the monkey released the lever on matching trials (within 500 ms of test stimuli onset) or kept the lever depressed for 750–1000 ms on nonmatching trials.

attended mode, the animal reported whether the orientation of the stimuli in the receptive field matched. However, in the unattended mode, the animal reported whether the colors of the stimuli outside the neuron's receptive field matched. This was called the space-andfeature attention task because the neuronal correlate for attention that we measured could depend on either the animal shifting its attention between different locations or different features (color or orientation).

Because only some neurons in area V4 have clear attentional modulation, we selected those cells that showed attentional modulation during the space-and-feature attention task (McAdams and Maunsell 1999). For these neurons, data were collected in blocks of one task (spatial or space-and-feature) and one behavioral state (attended or unattended). The animal was instructed to attend to stimuli at only one location using instruction trials in which visual stimuli appeared at only one location. After the animal performed two instruction trials correctly, the other stimuli returned. He continued to direct his attention to the instructed location until a new instruction trial was provided. The initial condition was randomly selected and the 4 conditions were performed in blocks of 16 correct trials, with at least 2 cycles of each condition obtained for each neuron. Trials were balanced within each task so that each of the four stimulus-behavioral combinations was equally likely. Trials were aborted if the animal broke fixation or released the lever before the stimulus appeared.

Neuronal Recording and Data Collection

Data were collected from area V4 in both animals using recording chambers (20 mm diam) that were implanted on intact skull over V4. One animal received a second V4 chamber so that data were collected from three hemispheres in two animals. Transdural recordings were made using Pt/Ir recording electrodes of 1–2 M Ω at 1 kHz. Signals from the microelectrode were amplified, filtered, and monitored on an oscilloscope and an audio monitor. Histological reconstructions of the recording areas showed that all recordings were in V4 in the anterior part of the prelunate gyrus, dorsal to the end of the inferior occipital sulcus.

One stimulus was centered in the receptive field of the neuron being recorded and the other stimulus was placed at equal eccentricity diametrically across the fovea. The contrast of the Gabors was temporally counterphased at 4 Hz with a sinusoidal profile. The receptive field centers of the V4 neurons were located between 1.2° and 5° eccentricity. Receptive fields were plotted using a task in which the animal maintained fixation on a central spot of light while the exper-

imenter moved a small bright bar while listening to the neuronal response on the audio monitor. Stimuli were generally larger than the receptive fields of the neurons. The oriented patches were adjusted in spatial frequency, color, and size to produce optimized responses. The unattended oriented patches had the same parameter values as the attended oriented patches.

RESULTS

We examined the effects of these tasks on 71 isolated neurons in area V4 in 2 monkeys. Most of the neurons showed significant attention effects [62/71 cells; three-factor analysis of variance (ANOVA); P < 0.05] and most were orientationselective (60/71 cells; three-factor ANOVA; P < 0.05). The specific task the animal performed significantly affected the firing rate of 31% of the neurons (22/71 cells; three-factor ANOVA; P < 0.05). We found relatively few cells with individually statistically significant interactions between attention and task (7/71 cells), task and stimulus orientation (8/71 cells), and attention, task, and stimulus orientation (6/71 cells). However, 48% of the neurons (34/71 cells) showed an interaction between attention and stimulus orientation. We have previously reported that attention causes a proportional increase in the responses of these neurons, using different orientations to elicit different response levels (McAdams and Maunsell 1999). Because small absolute effects of attention were found at orientations away from the peak of the tuning curve, the rest of this analysis was restricted to the data obtained when the preferred orientation of the neuron was in the receptive field.

The responses of two single units are plotted in Fig. 2. The visual stimulation of each neuron was the same within each task and the receptive field stimulus was the same in all conditions, but the stimulus outside the neuron's receptive field differed between the two tasks. Each unit responded more strongly when the animal was attending to the stimulus in the receptive field. Although the unit in Fig. 2A responded more strongly overall during the spatial task, it was more modulated by attention in the space-and-feature task. This neuron appeared to receive feature-dependent attentional modulation as well as spatial attentional modulation. The unit in Fig. 2B showed the same amount of attentional modulation in both tasks, presumably reflecting spatial attention alone.

We calculated an attention index, (attended response unattended response)/(attended response + unattended response), for each neuron in each task. The population of neurons showed consistently more modulation in the spaceand-feature attention task than in the spatial attention task (Wilcoxon signed rank test, P < 0.001). The median attention index during the spatial attention task was 0.13, corresponding to a 31% increase in activity and the median attention index during the space-and-feature attention task was 0.21, corresponding to a 54% increase in activity. Although we selected cells showing attention effects in the space-and-feature attention task, we could have found neurons without attention effects in the spatial attention task. Notably, every neuron that we recorded with a positive attention effect in the space-andfeature attention task also had a positive attention effect in the spatial attention task, although not all of these effects were statistically significant. This suggests that appreciable attentional modulation for features may not occur in isolation under these conditions.



FIG. 2. Responses of 2 neurons for the 4 conditions. Each set of 4 histograms corresponds to the averaged responses obtained from presenting the same visual stimulus (preferred orientation for each cell) in the receptive field of a given neuron for each task condition and each behavioral mode. *y* axis of each histogram is firing rate in spikes/s; *x* axis is time during the trials. Average response rate is computed for entire period during which the sample stimulus is on (shaded gray period). Average responses in the sample period for each task condition and behavioral mode are displayed in the upper right of each histogram. Unit in *A* showed increased attentional modulation during the space-and-feature attention task (52%) compared with the attention modulation during the spatial attention task (21%). Unit in *B* showed the same amount of attentional modulation during the 2 tasks (38%).

Although the same stimulus appeared inside the receptive field in all conditions, the distant stimulus differed between the two task modes. That stimulus was far outside the classical receptive field of the neuron being recorded but might have affected the responses between conditions. To examine this possibility, we compared the responses to the attended modes in both tasks. In both of the "attended" conditions, the animal attended to an oriented stimulus inside the receptive field and only the distant unattended stimulus differed. Responses were not significantly different between these conditions (Fig. 3A) suggesting that the distant retinal stimulus was not a factor by itself (median space response 23.6 spike/s; median space-andfeature response 24.5 spike/s; Wilcoxon signed rank test, P >0.99). When the animal attended to the distant site, however, the feature being attended did affect responses (Fig. 3B). In the unattended modes, attention was directed to orientation during the spatial task and attention was directed to color during the space-and-feature task. Responses were significantly greater in the spatial attention task than in the space-and-feature attention task (median space response 16.4 spikes/s; median space-andfeature response 14.8 spikes/s; Wilcoxon signed rank test, P <0.001). Thus the change in attentional modulation was a result of the differences in the behavioral requirements in the unattended mode, which resulted in decreased neuronal responses to the oriented grating when the animal was performing the color task, relative to the neuronal responses to the oriented grating when the animal was performing the orientation task on a different grating.

An alternative explanation for these results is that the animal might have been less challenged and therefore less vigilant when matching color compared with matching orientation. This could cause the weaker responses during the unattended mode of the space-and-feature task which we observed. One way to assess whether task difficulty has significantly affected the neuronal responses is to examine whether the magnitude of the neurophysiological attentional modulation is correlated with the magnitude of differences in the behavioral performance between the attended and unattended conditions during the space-and-feature task. We assessed behavioral performance based on the accuracy of the animal's responses to completed trials. The behavioral performance of the two animals during the space-and-feature task ranged from 77% to 91%, with a median of 84%. We calculated a behavioral performance index, (attended performance - unattended performance)/(attended performance + unattended performance), for each cell. We then examined whether there was any significant correlation between the neurophysiological attentional index, as previously described, and the behavioral performance index. We found no significant correlations between these indices (r = -0.33; P > 0.75), suggesting that the neurophys-



FIG. 3. Change in attentional modulation depends on the change in behavioral state. Responses to the preferred orientation collected during the space-and-feature attention task are plotted against responses to preferred orientation collected during the spatial attention task for attended (*A*) and unattended (*B*) modes. No difference in responses was found during the attended modes (Wilcoxon signed rank test, P >0.99) but responses were different in unattended modes (Wilcoxon signed rank test, P < 0.005). iological difference observed is unlikely a result of a difference in difficulty in performing the two types of tasks.

As a more direct test of the effects of task difficulty, we recorded from 23 neurons in 1 animal using 2 versions of the spatial attention task, which differed in the difficulty of the orientation matching. In one version, the task was easy because the nonmatching stimuli differed in orientation by 90° and the animal's performance was high, 89% correct. The other version of the task was more difficult because the nonmatching stimuli differed in orientation by 30° and the animal's performance was worse, 75% correct. However, there was no significant difference between attentional effects measured for these cells in the easy and difficult variants (Wilcoxon signed rank test, P = 0.98) despite the fact that these cells did show significant attention effects in both the easy and difficult tasks (Wilcoxon signed rank test, P < 0.05). These results support the interpretation that the increased attentional modulations seen in the space-and-feature attention task relative to the spatial attention task were due to the difference in attending to different stimulus features rather than a difference in task difficulty.

DISCUSSION

These experiments contribute to understanding how different forms of attention interact in visual processing. They show that spatial attention and feature attention coexist in a relatively early stage of visual processing, cortical area V4. This finding is consistent with the demonstrations of attentional modulations in area V4 both by tasks requiring spatial attention (Connor et al. 1996, 1997; Moran and Desimone 1985; Motter 1993) and by tasks that require feature-directed attention (Haenny and Schiller 1988; Haenny et al. 1988; Maunsell and Hochstein 1991; Maunsell et al. 1991; Motter 1994a,b). Further, they indicate that the same neuron can receive multiple types of attentional inputs.

We have also suggested that when attention is directed to an oriented stimulus at a particular location, oriented neurons with receptive fields throughout the visual field show a relative increase in activity. Motter (1994a) has previously shown that V4 neuronal responses can be enhanced when the color or luminance of the neuronal stimulus in the receptive field matches the color or luminance of a cue. However, in that experiment, the stimulus in the receptive field could become the target. In our experiment, the process of attending to orientation affected the signals of neurons throughout the visual field even when those neurons appear to be irrelevant to the task. An alternative explanation is that attention to the colored stimuli suppresses the responses of neurons to oriented stimuli. Either interpretation shows that directing attention to a stimulus feature might modulate the responses of neurons throughout the visual field. These results provide neurophysiological evidence that visual attention may be allocated by a segmentation of the scene consistent with Gestalt principles of perceptual organization: the neuronal responses to the distractor grating are increased when attention is directed to another grating than when attention is directed to a color patch.

Recently, Treue and Trujillo (1999) reported that neurons in area MT could be modulated by both spatial and feature-

directed attention. They presented two random dot stimuli, one inside and one outside of the receptive field of the neuron being recorded. The monkeys were cued to attend to a particular location. They then examined the effects of changing the direction of the motion of the stimulus outside the receptive field on the neuronal responses to the stimulus in the receptive field. They found no effect of changing the stimulus outside the receptive field unless the animal was attending to it, just as we have reported for V4 neurons in this experiment. In their task, when the animal attended to the stimulus outside the receptive field and it was moving in the preferred direction for the neuron being recorded, the neuron's responses were 13% greater than when the stimulus outside the receptive field was moving in the null direction. In our analogous condition, we found an 11% increase in response when the animal attended to the orientation of the stimulus outside the receptive field rather than its color. Both of these results suggest that processing features even of a specific target may require dynamic comparisons using information obtained from other stimuli in the visual field.

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