

Responses in Area V4 Depend on the Spatial Relationship Between Stimulus and Attention

CHARLES E. CONNOR, JACK L. GALLANT, DEAN C. PREDDIE, AND DAVID C. VAN ESSEN

Department of Anatomy and Neurobiology, Washington University School of Medicine, St. Louis, Missouri 63110

SUMMARY AND CONCLUSIONS

1. We studied the spatial interaction between stimulus and attention in macaque area V4. Monkeys were required to fixate a small spot while continuously attending to a ring-shaped target within a large array of identical rings. Meanwhile, the response of the V4 cell under study was tested by flashing behaviorally irrelevant bar stimuli in the cell's classical receptive field (CRF). The location of the attended ring was varied across four positions surrounding the CRF, and the location of the bar stimulus was varied across five positions spanning the CRF.

2. Response strength depended on two aspects of the spatial relationship between the stimulus driving the cell (the bar) and the position of attention (the target ring). First, for 49% of the cells studied, responses were greater for bar stimuli near the attended ring; i.e., the receptive field profile shifted toward the attentional focus. Second, for 84% of the cells, the overall response level depended on the direction in which attention lay relative to the stimulus in the CRF (e.g., to the left, right, above, or below).

3. This study confirms a key prediction of spatial models of attention, which postulate enhanced processing of all stimuli near the attentional focus. It also introduces the novel finding that responses are influenced by the relative direction of attention. This result indicates that area V4 carries information about the spatial relationship between visual stimuli and attention.

INTRODUCTION

Focal attention involves selective visual processing of a given object (Duncan 1984) or region of space (Posner et al. 1980). Previous experiments in visual cortical areas related to object recognition (areas V1, V2, V4 and inferotemporal cortex) have shown that neural responses to attended stimuli are generally stronger than responses to nonattended stimuli (Moran and Desimone 1985; Motter 1993), consistent with either object-based or spatial selectivity. We sought to characterize the specifically spatial aspects of attentional modulation in area V4 by systematically and independently varying the position of attention and the position of the stimulus used to evoke responses.

METHODS

Our behavioral paradigm involved two display items, one to control attention and the other to probe responses. The attended target was a ring, drawn with a narrow line in a color that was nonoptimal for the cell. The probe stimulus was a behaviorally irrelevant bar of optimal color, width, and orientation. Each behavioral trial began with the appearance of a fixation spot and a field of rings on the video monitor facing the monkey (Fig. 1). The

animal was required to fixate within a 0.5°-diam window (fixation was monitored with a scleral search coil) and depress a response lever. The attended ring was identified by a slightly delayed onset (500 ms after fixation). Attended ring position was varied across the four locations surrounding the classical receptive field (CRF). The animal was trained to release the response lever when, after a variable time interval (0.5–4.5 s), a quadrant of the attended ring disappeared (the ring became C-shaped). Catch trials, in which one or more rings at noncued positions changed shape before the attended ring, were included to ensure that attention was concentrated on the cued location. Bars were flashed (for 150 ms each) one at a time in random order at five locations spanning the CRF. Bars were presented at 1-s intervals beginning 1 s after attended ring onset. Recordings were made from 88 cells in area V4 of two macaque monkeys (one *Macaca nemestrina* and one *Macaca mulatta*). Single-cell responses were recorded with epoxy-coated tungsten electrodes (A-M Systems) introduced transdurally through a 5-mm diam craniotomy with a stepping motor microdrive (Caltech Central Engineering Services). The electrical signal was collected through the audio channel of an Iris Indigo workstation (Silicon Graphics), which was also used to control behavior and stimulus presentation.

RESULTS

We observed two major effects relating to the spatial interaction between stimulus and attention. The first was a shift of the response profile toward the attended ring. For the cell shown in Fig. 2A, the peak response region was shifted to the right (in the figure) when attention was directed to the right, and to the left when attention was directed to the left. The response profile was roughly centered for the other two attention positions. This effect was quantified by measuring the fraction of total response strength shifting from one half of the CRF to the other as attention was shifted along the same axis (see legend to Fig. 2). The fractional shift for this cell was 0.41. Across the population of cells (Fig. 2B) response shifts were weighted in the direction of attention (positive values), with a mean shift value of 0.16. Two-tailed *t*-tests using randomization methods (Manly 1991) showed that 49% (43 of 88) of the cells underwent a significant ($P < 0.05$) shift in response strength toward the attended location; only one cell showed a significant shift in the opposite direction (significant shifts are indicated by the filled bars in Fig. 2B).

The second effect we observed was a change in overall response magnitude depending on the direction of attention relative to the receptive field. In the example shown in Fig. 3A, responses were strong when attention was directed below or to the left of the receptive field and weak

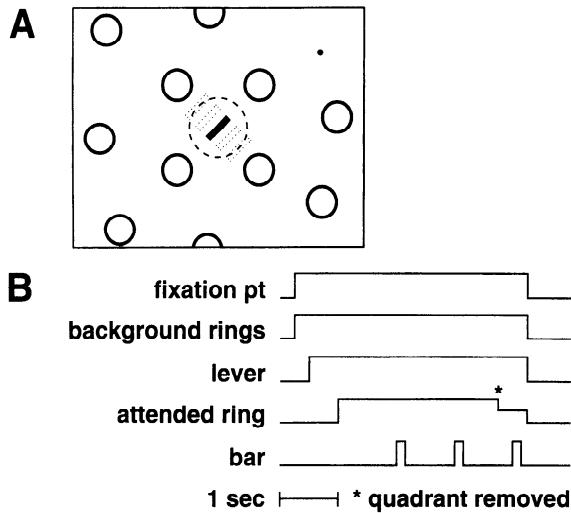


FIG. 1. Stimulus display and behavioral paradigm. *A*: video display. Small dot: fixation point. Dashed circle (which was not visible on the screen): classical receptive field (CRF) of the cell under study. The CRF was mapped before the attention test using a bar stimulus under the experimenter's control, while the monkey performed a simple fixation task. For some cells the CRF location was confirmed with an automated receptive field plotting program. In the attention task, bars were presented at 5 positions spanning the CRF at intervals of 0.25 CRF diameters (dotted outlines). Only 1 position (filled bar) was tested at a time. Bar length was 0.5 CRF diameters. Attended rings were presented at 4 positions defined relative to the optimal bar orientation and offset from the center of the CRF by 1 diameter. Rings were 0.5 CRF diameters in size and 0.1° in width. *B*: time lines showing the sequence of events during a typical trial (see text for details). The attended ring position was cued by a delayed onset (500 ms after fixation). To increase the animal's certainty about where to attend, the position of the cued ring was blocked in sets of 12 trials. The animal was required to release the response lever within 700 ms when a randomly positioned quadrant was removed from the attended ring. Bars were presented at 1-s intervals even after the change in the attended ring so as not to provide the animal with a secondary cue. Bar presentations occurring later than 0.5 s before the change in the attended ring or during catch trials were not included in the analysis.

when attention was directed above or to the right. Directional attention effects of this kind were quantified by summing responses across bar positions for each attention position, finding the maximum and minimum summed responses, and expressing the difference as a fraction $[(\max - \min)/\max]$. The fractional response difference for the example cell in Fig. 3*A* was 0.84. The distribution of fractional differences for the population of cells is shown in Fig. 3*B*. The mean fractional difference was 0.56. The expected mean value if there were no effect of attention, based on the observed variability in response rates, was calculated to be 0.26 (arrow). Analysis of variance using randomization methods showed that attention position had a significant main effect ($P < 0.05$) on response strength for 84% (74 of 88) of these cells (filled bars in Fig. 3*B*). The optimal attention positions were not biased toward any particular direction (e.g., left, right, up, down, foveal or peripheral).

DISCUSSION

The two phenomena described here bear on the mechanisms and functions of attention in area V4, an important intermediate stage in the object recognition pathway of

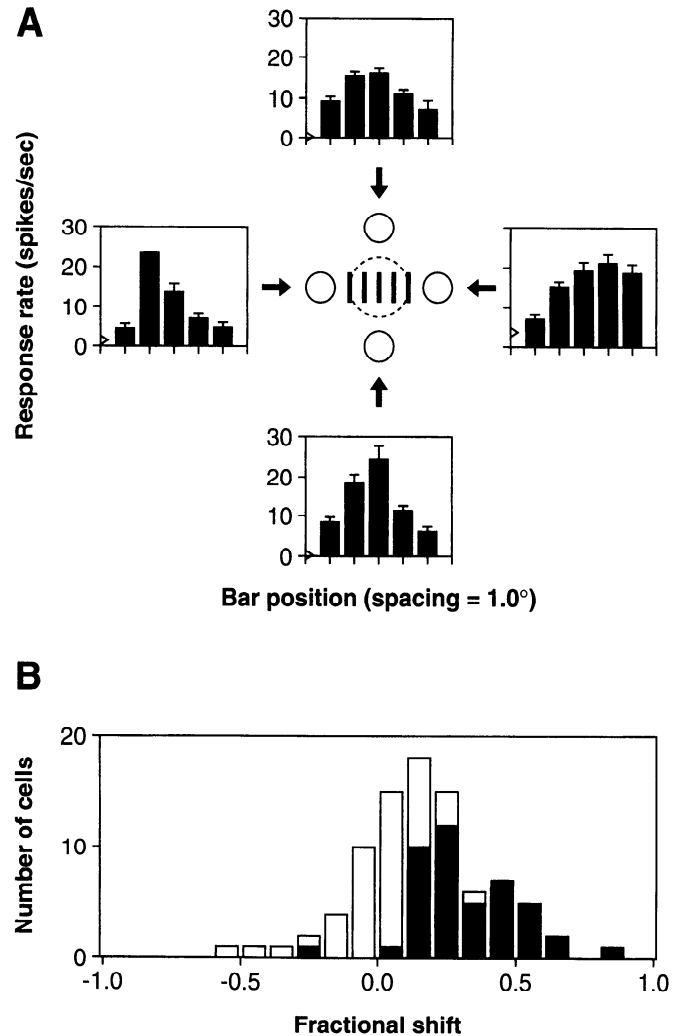


FIG. 2. Response profile shift. *A*: single cell example. Each of the 4 plots represents the response profile of the cell as the animal was attending to the ring stimulus indicated by the arrow. Average responses and standard errors are based on 8 repetitions at each bar position. Response rates were calculated across a 450-ms time window beginning ~ 25 ms after bar onset. Background response rates (arrowheads on left axes) were based on equivalent time periods scattered randomly through the behavioral run in which no bar stimulus was presented. This cell's plotted CRF was 4.0° diam and was located 3.7° below and 3.3° to the right of fixation. Bar orientation was horizontal, so the plot at the left actually corresponds to an attended ring above the CRF, etc. *B*: population results for 88 cells. This plot shows the distribution of shift effects across 88 cells. The response profile shift for each cell was quantified by separately summing responses to bars on the left and right halves of the profile and calculating what fraction of the total response accrued to each half (the center bar was excluded from this analysis). The change in these fractions as attention was directed to the left or right (i.e., along the axis orthogonal to bar orientation) was defined as the fractional shift. A positive value reflects a shift of the response profile in the same direction as attention. Significance was assessed using a 2-tailed randomization *t*-test in which the test statistic was the fractional shift value. A randomized distribution was generated by permuting the original response values across attention position and recalculating the test statistic 10,000 times. Cells showing effects significant at the 5% level are plotted in black. Population results shown here and in Fig. 3 were based on prior subtraction of the background response rates, but comparable results were obtained without background subtraction.

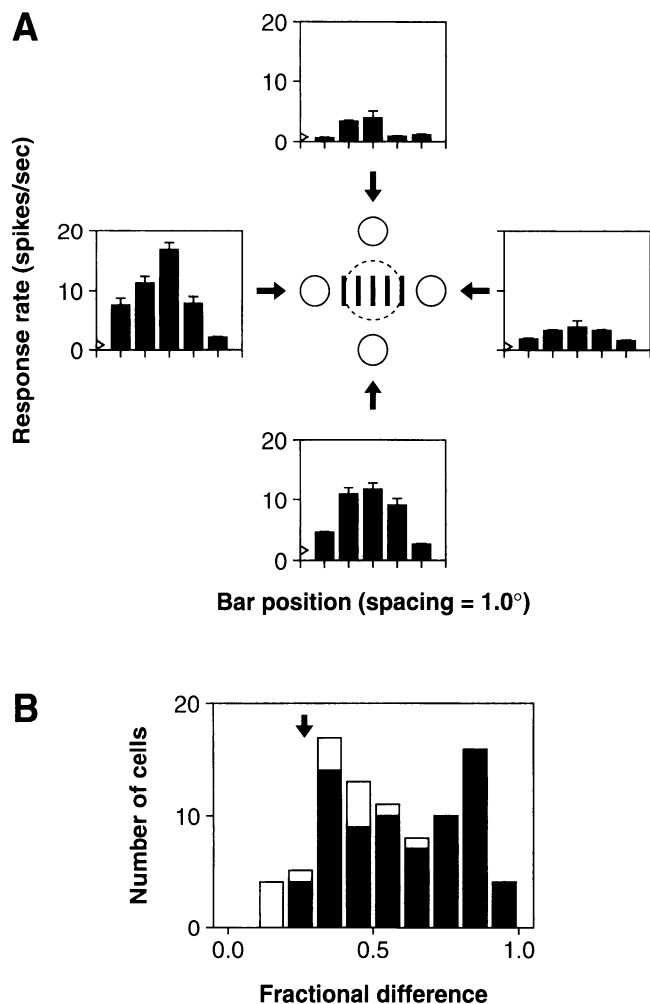


FIG. 3. Directional attention effect. *A*: single cell example. This cell's plotted CRF was 3.8° diam and was located 4.2° below and 4.6° to the right of fixation. Bar orientation was 30° counterclockwise from vertical. Other details as in Fig. 2. *B*: population results for 88 cells. As described in the text, the directional effect for each cell was quantified by finding the fractional difference in total response between the two attention conditions producing maximum and minimum responses. Significance was calculated by means of randomization analysis of variance in which the test statistic was squared response total summed across the 4 attention positions (which is equivalent to an F ratio in this method). Cells showing effects significant at the 5% level are plotted in black. Arrow: expected mean fractional difference if there were no effect of attention, as calculated in the randomization analysis. It might be postulated that the effects shown here are somehow due to the sensory transient introduced by the onset of the attended ring 1 s before the 1st bar presentation. If so, the effects would presumably be strongest for the 1st bar presentation and decay thereafter. But in fact, for cells showing significant directionality, the average fractional difference was slightly greater at the 2- and 3-s timepoints (0.64) than at the 1-s timepoint (0.60).

visual cortex. The enhancement of responses to irrelevant stimuli near the attentional focus (Fig. 2) provides direct evidence for a specifically spatial mechanism of attention—a spotlight of enhanced processing centered on the attended object that affects other stimuli within its scope. Previous demonstrations of enhanced responses to the attended stimulus itself (Moran and Desimone 1985; Motter 1993) are compatible with both spatial and object-specific

mechanisms. Our result does not exclude the possibility of an additional, object-specific enhancement that would apply exclusively to the attended object and not to other stimuli in the same region of space (Duncan 1984).

The observation that response strength depends on the direction in which attention lies relative to the stimulus (Fig. 3) is not anticipated by standard spotlight (Posner et al. 1980) or response competition (Desimone and Duncan 1995) models of attention. The functional implication of this phenomenon is that area V4 carries information about the spatial relationship between stimulus and attention. Such information is potentially useful for representing the position of visual features within a local reference frame centered on the attended object. Recent psychological results provide evidence for object-centered processing (Driver et al. 1992; Gibson and Egeth 1994; McCloskey and Rapp 1995; Tipper et al. 1991). The directional attention effects reported here may reflect an intermediate stage in a neural transformation from retinal to object-centered coordinates; this transformation would culminate in response fields that maintain a fixed position with respect to the attentional focus (Olshausen et al. 1993; cf. Olson and Gettner 1995).

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Address reprint requests to D.C. Van Essen.

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