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Report

Time Course of Attention Reveals Different Mechanisms for Spatial and Feature-Based Attention in Area V4

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Summary

Attention can facilitate visual processing, emphasizing specific locations and highlighting stimuli containing specific features. To dissociate the mechanisms of spatial and feature-based attention, we compared the time course of visually evoked responses under different attention conditions. We recorded from single neurons in area V4 during a delayed match-to-sample task that controlled both spatial and feature-based attention. Neuronal responses increased when spatial attention was directed toward the receptive field and were modulated by the identity of the target of feature-based attention. Modulation by spatial attention was weaker during the early portion of the visual response and stronger during the later portion of the response. In contrast, modulation by feature-based attention was relatively constant throughout the response. It appears that stimulus onset transients disrupt spatial attention, but not feature attention. We conclude that spatial attention reflects a combination of stimulus-driven and goal-driven processes, while feature-based attention is purely goal driven.

Introduction

Attention can selectively enhance sensory processing of different aspects of the visual world (Reynolds and Chelazzi, 2004; Desimone and Duncan, 1995). Spatial attention controls the selection of specific locations in the visual field (McAdams and Maunsell, 1999; Reynolds et al., 1999); feature-based attention controls selection of object attributes such as color and orientation (Motter, 1994; Treue and Martinez Trujillo, 1999). Are these two forms of attention mediated by the same neural mechanisms? Some have argued that spatial position and other stimulus properties are processed similarly by a general attentional control system (Maljkovic and Nakayama, 1996; Bundesen, 1990). Others have suggested that the retinotopic organization of early and intermediate visual areas may affect the representation of spatial attention (Shih and Sperling, 1996; Tsal and Lavie, 1993; Lamy and Tsal, 2001). Determining the relationship between spatial and feature-based attention is essential for understanding how attention facilitates the transformation from the retinotopically organized representation in primary visual cortex (De Valois and De Valois, 1990) to the object- and feature-based representation found in inferior temporal areas (Tanaka, 1996).

Psychophysical studies suggest that the timing of modulation of visually evoked responses may differ for spatial and feature-based attention. Spatial attention appears to be disrupted briefly by the abrupt appearance of visual stimuli (Nakayama and Mackeben, 1989; Egeth and Yantis, 1997). In contrast, it is unclear whether feature-based attention is disrupted in the same way (Lamy and Tsal, 2001). If the dynamics of the effects of spatial and feature-based attention on the visual response are different, it would support the idea that these two forms of attention are mediated by different neural mechanisms.

To determine whether spatial and feature-based attention are governed by similar neural mechanisms, we compared the time course of their modulatory influence on visually evoked responses. If spatial and feature-based attention are controlled by a common neural substrate, they should evolve similarly over time; any difference in their temporal evolution would suggest that they are mediated by different neural mechanisms.

Results

Responses were recorded from 110 V4 neurons in two macaques while they performed a delayed match-to-sample task (see Figure 1A or Movie S1 in the Supplemental Data available with this article online). The task controlled both spatial and feature-based attention while two streams of rapidly changing natural image patches appeared at two locations in the visual field. The time course of neuronal responses to the distractor patches that appeared in the receptive field was analyzed. Responses to both match and catch patches were excluded from the analysis. Spatial attention and feature-based attention were both controlled on every trial. To quantify the effects of spatial attention, responses were averaged across the two feature conditions; to quantify the effects of feature-based attention, we averaged responses across the two spatial conditions (see Figure 1B). A two-factor ANOVA revealed that there was a significant interaction in almost half of the cells, but its magnitude was small. Because the interaction is not directly relevant to this paper, the rest of the paper is concerned with the main effects of spatial and feature-based attention.

Time Course of Response Modulation by Spatial Attention

Figure 2A shows the average responses of one V4 neuron to all distractors when attention is directed toward versus away from the receptive field. Responses are aligned to distractor onset. The location of spatial attention modulates responses in 74% of cells (n = 81/110; randomized t test, $p < 0.05$). Responses are generally greater when spatial attention is directed toward the receptive field than when it is directed away. This difference is visible at the earliest stages of the visually

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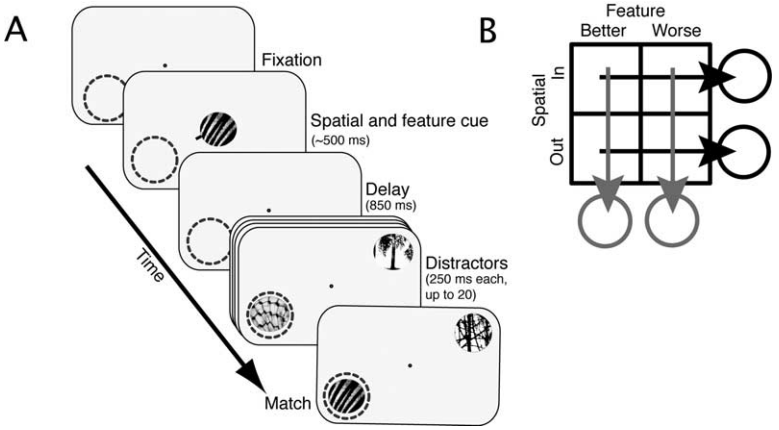

Figure 1. Delayed Match-to-Sample Task and Analysis

(A) Each frame represents a different portion of the trial. Dashed circle represents the receptive field of the neuron under study. A target (feature cue) appeared at the fixation spot for 150–600 ms. A small red line (spatial cue) appeared on one side of the target to designate the relevant stream (for the majority of cells, the spatial cue was only shown on the first trial in each block). Following an 850 ms delay period, two streams of patches appeared, one in the receptive field and one in the opposite quadrant. Patches were shown at approximately 4 Hz with no blank interval between successive patches. Reward was given for bar release within 1 s after the target appeared in the cued stream. Failures to release, early releases, and fixation breaks at any time were considered errors. The target and all distractors were circular patches selected from photos and fit to the size of the neuron's receptive field.

(B) There were four attention conditions consisting of a cross of two spatial and two feature conditions. Spatial attention comparison (black lines) was performed by averaging data collected over the two feature conditions; feature-based attention comparison (gray lines) was performed by averaging data collected over the two spatial conditions.

evoked response and continues throughout the entire response period. Note that because responses are aligned to stimulus onset (not trial onset), any modulation that occurs before the transient response must reflect the influence of the previous stimulus. It is not due to delay period activity.

The difference between the two peristimulus time histograms (PSTHs) shown in Figure 2A is given in Figure 2B. Spatial attention modulates responses by about 15% on average (8 spikes/s), but this modulation changes over time. Soon after stimulus onset (100–150 ms; first black bar at bottom of graph), the modulatory influence of spatial attention drops significantly, to about 5% (3 spikes/s). After about 50 ms, modulation returns to 15%. This pattern is fairly common in V4 neurons. Across the sample, the magnitude of spatial attention decreases during the early portion of the response (usually 100–150 ms) in approximately one-third of cells (36/110, 33%; randomized t test, $p < 0.05$) and increases in fewer than 2% (2/110; randomized t test, $p < 0.05$) of cells. This effect occurs significantly more often than would be expected by chance (chi-square test, $p < 0.001$).

Figure 2C shows the average temporal profile of all 110 V4 neurons in the sample (including those that are not significantly modulated), and the difference is given in Figure 2D. (Averaging was performed on raw spike rates rather than normalized rates; similar results are obtained with normalized rates.) Across the sample, the average modulatory effect of spatial attention is about 20%; this is reduced to less than 10% during the early portion of the response.

The brief reduction in modulation effectively disrupts the sustained enhancement associated with spatial attention. For this reason we call it attentional disruption. Figure 2E shows a histogram of the size of the spatial attention disruption across the sample, obtained by subtracting spatial attention modulation in the early and late portions of the response of each cell. The histogram is shifted to the left significantly (randomized t test, $p < 0.001$), indicating that attentional modulation is generally diminished during the early portion of the response.

Time Course of Response Modulation by Feature-Based Attention

The data presented thus far show that spatial attention is briefly disrupted soon after the onset of each distractor. We used an analogous procedure to determine whether stimulus transients disrupt feature-based attention. Responses are significantly modulated by feature-based attention in 69% of cells (n = 76/110; randomized t test, $p < 0.05$). Figure 3A compares the temporal responses of one V4 neuron (the same cell shown in Figure 2A) when feature-based attention is directed toward each target. The difference between the PSTHs shown in Figure 3A is given in Figure 3B. When feature-based attention is directed toward the more effective target, responses are about 10% higher than when it is directed toward the less effective target. In contrast to the results obtained for spatial attention, this modulation does not vary significantly over time; the amount of modulation is the same during the early and late portions of the response.

The time course of response modulation by feature-based attention illustrated in Figures 3A and 3B is typical for V4 neurons. When feature-based attention is directed toward a more effective target, the average response is about 10% larger than when it is directed toward a less effective target. This modulation is consistent throughout the response period. Across the sample, most neurons show stable modulation over time (89/110, 81%; randomized t test, $p > 0.05$). The remaining neurons (21/110, 19%; randomized t test; $p < 0.05$) are about evenly split between those that show enhancement (n = 10; randomized t test, $p < 0.05$) and those that show suppression (n = 11; randomized t test, $p < 0.05$) during the early part of the response. There is no statistically significant trend in one direction or the other across the sample (randomized t test, $p > 0.05$).

The average temporal response of all 110 cells in the sample is shown in Figures 3C and 3D (format same

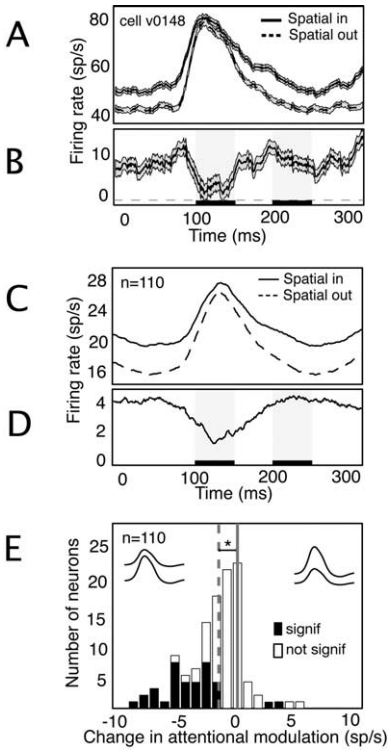

Figure 2. Effects of Spatial Attention Are Reduced during the Early Portion of the Response

(A) Peristimulus time histograms (PSTHs) for one V4 neuron show the average stimulus onset-aligned response to the set of distractors (pooled over different distractors) when spatial attention is directed toward (solid line) or away from (dashed line) the receptive field. Width of shaded region indicates one standard error above and below the mean. Time zero indicates the time of distractor onset. Modulation by spatial attention is smaller during the early portion of the response (100–150 ms) and greater at longer time lags (200–250 ms). Note that because responses are aligned to stimulus onset, modulation prior to the transient response reflects modulation for the previous stimulus, not delay period activity.

(B) Difference between the responses in the two spatial attention conditions shown in (A), emphasizing the pattern of modulation over time. The black bars below the curve indicate the two time periods used in the analysis.

(C) The time course of spatial attentional modulation of the visually evoked response, averaged over the entire sample of 110 V4 neurons. Format same as in (A). PSTHs have been aggregated from raw responses without normalization. Modulation is lowest during the early portion of the response.

(D) Difference curve giving the magnitude of spatial attention modulation over time for all cells in the sample. Format same as in (B).

(E) Histogram of response modulation (see Experimental Procedures). Cells falling to the left of zero have smaller modulation during the early portions of the response than during the late portions of the response. Black bars indicate cells that are significantly modulated. Vertical dashed line indicates the median value. Cartoons represent typical PSTHs of neurons on either side of the histogram. Cells with significant modulation (black bars) are more likely to show suppressed modulation during the early portion of the response.

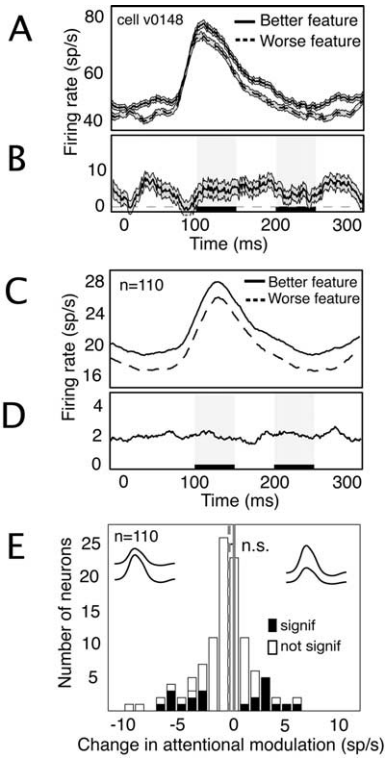

Figure 3. Effects of Feature-Based Attention Are Constant throughout the Response

(A) Peristimulus time histograms (PSTHs) for one V4 neuron show the average stimulus onset-aligned response to the same set of distractors (pooled over different distractors) when feature-based attention is directed to the more effective target ("better feature"; solid line) or the less effective target ("worse feature"; dashed line). Time zero indicates the time of distractor onset. For this neuron, modulation by feature-based attention is constant throughout the response period. Note that because responses are aligned to stimulus onset, modulation prior to the transient response reflects modulation for the previous stimulus, not delay period activity

(B) Difference between the responses in the two feature-based attention conditions shown in (A). At no time does the modulation drop significantly.

(C) The time course of feature-based attentional modulation of the visually evoked response averaged over the entire sample of 110 V4 neurons. Format same as in (A). PSTHs have been aggregated from raw responses without normalization. Modulation is constant throughout the response.

(D) Difference curve giving the magnitude of feature-based attention modulation over time for all cells in the sample. Format same as in (B). At no time does the modulation drop significantly.

(E) Histogram of response modulations (see Experimental Procedures). Cells falling to the left of zero have smaller modulation during the early portions of the response than during the late portions of the response. Black lines indicate cells that are significantly modulated. Vertical dashed line indicates the center of mass of the histogram. Cartoons represent typical PSTHs of neurons on either side of the histogram. Cells with significant modulation (black bars) are equally likely to show enhanced and suppressed modulations during the early portion of the response.

as Figures 2C and 2D). The solid line represents the response to distractors obtained when the more effective target (estimated separately for each cell) is attended; the dotted line gives the average response when the less effective target is attended. Across the sample, there is no indication that the effect of feature-based attention changes over time.

Figure 3E shows a histogram of the strength of attentional disruption across the sample. The center-of-mass

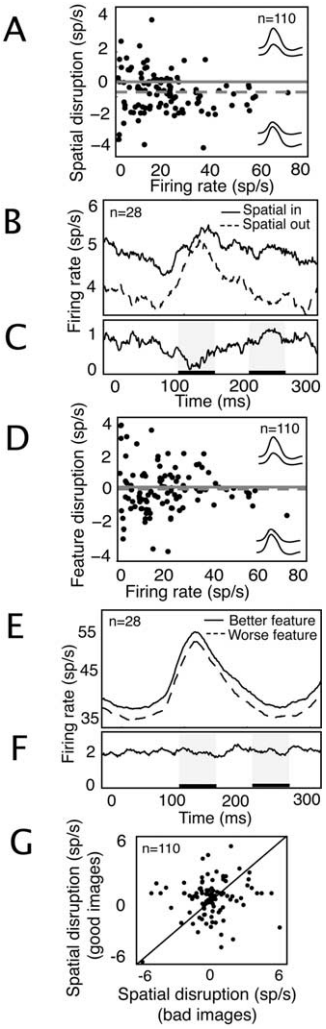

Figure 4. Attentional Disruption Does Not Correlate with Firing Rate

(A) Scatter plot of spatial attention disruption and firing rate. Each dot represents one cell. Horizontal axis shows mean firing rate of cell; vertical axis shows magnitude of attentional disruption, normalized by cell's mean firing rate (see Experimental Procedures). Cartoons represent typical PSTHs of neurons on either side of the plot. Disruption is not correlated with the mean firing rate of the cell.

(B) PSTHs for the subsample of 25% of cells with the lowest firing rates. Format same as in Figure 2B. Spatial attention is disrupted even in cells with the lowest firing rates.

(C) Difference between the responses in the two spatial attention conditions shown in (B), emphasizing the time course of attentional modulation.

(D) Scatter plot of feature-based attention disruption and firing rate. Each dot represents one cell. Horizontal axis shows mean firing rate of cell; vertical axis shows magnitude of attentional disruption, normalized by the cell's mean firing rate (see Experimental Procedures). Strength of feature-based attention disruption is not correlated with the mean firing rate of the cell.

(E) PSTHs for a subsample of the 25% of the cells with the highest firing rates. Format same as in Figure 3B. Feature-based attention is not disrupted even in the cells with the highest firing rates.

(F) Difference between the responses in the two feature-based attention conditions shown in (E), emphasizing the time course of attentional modulation.

(G) Spatial attention is disrupted by patches that are less effective in driving the cell. Scatter plot showing magnitude of attentional disruption for the subset of patches evoking weaker and stronger responses. Attentional disruption is equally strong in both conditions.

of this histogram is not significantly different from zero (randomized t test, $p > 0.05$), indicating that feature-based attention is stable over time. This distribution is significantly different from the distribution associated with spatial attention (chi-square test, $p < 0.001$).

Attention Effects Do Not Depend on Firing Rate

Many neurons in the visual system give a strong transient response soon after stimulus onset, followed thereafter by a sustained response of lower magnitude. The transient response can be quite large, often exceeding a rate of 100 spikes per second for a brief period (Dean et al., 1982; David et al., 2004). If the transient response represents the maximum firing rate for a cell, then spatial attention cannot enhance firing during the transient (Treue, 2001). Thus, firing rate saturation would cause an apparent decrease in the modulatory effect of spatial attention during the early portion of the response. We performed three control analyses to test this response saturation hypothesis.

First, if the disruption in spatial attention is due to saturation, disruption should be larger in neurons with high firing rates. However, there is no significant correlation between the size of attentional disruption and the mean firing rate of each neuron (they are anticorrelated; $r = -0.11$; randomized t test, $p = 0.28$; see Figure 4A). In addition, the quartile of cells with the lowest firing rates ($n = 28$) still show a clear disruption in spatial attention during the response transient (Figures 4B and 4C).

If the disruption in spatial attention is an artifact of saturation, then we should also find a corresponding disruption in feature-based attention, and this should be stronger in cells with higher firing rates. Once again, there is no correlation between changes in the effect of feature-based attention and mean firing rate (they are anticorrelated; $r = -0.14$; randomized t test, $p = 0.14$; Figure 4D). The quartile of cells with the highest firing rates ($n = 28$) still show no change in the magnitude of feature-based attention over time (Figures 4E and 4F).

Finally, a saturation artifact should be strongest for distractors that evoke the highest firing rate from a cell. In fact, distractors that evoke responses greater than the median response for each neuron do not disrupt spatial attention any more than do distractors that evoke responses less than the median response (randomized t test, $p > 0.05$; Figure 4G). Taken together, these various controls demonstrate that the transient disruption in the effect of spatial attention is not due to response saturation.

Attention Effects Do Not Depend on Similarity of Target and Distractors

The data presented so far suggest that distractors disrupt spatial attention but not feature-based attention. It is possible that a subset of distractors do disrupt feature-based attention but their effects are averaged out. For spatial attention, distractors appear only at two locations, inside and outside the locus of spatial atten-

tion. For feature-based attention, distractors appear at many different locations in feature space. An additional control analysis was performed to test whether distractors most similar to or most dissimilar from the target disrupt feature-based attention. The efficacy of each distractor and target was assessed by averaging the neuronal response it evoked in all attention conditions. The subset of neurons for which one target evoked significantly greater firing than average and the other target evoked significantly less firing than average was extracted ($n = 19$; t test, $p < 0.05$). For these neurons, the 25% of distractors that evoked the greatest responses and the 25% of distractors that evoked the weakest responses were also extracted. Next, PSTHs for the two feature conditions were recalculated. In this control analysis, feature-based attention was not disrupted (randomized t test, $p > 0.05$). This suggests that the lack of disruption in feature-based attention is not due to the similarity between the distractors and the targets.

Discussion

We evaluated the relationship between spatial and feature-based attention by examining the time course of attentional modulation of the visually evoked response. Our results reveal a clear difference between these two forms of attention. Stimulus transients briefly decrease the enhancement caused by spatial attention but do not affect feature-based attention. This difference indicates that these processes are mediated, at least in part, by distinct neural mechanisms.

The brief decrease in the enhancement caused by spatial attention may reflect a temporary suppression of attention, or it may simply reflect a failure of additivity in the early part of the response. In either case, it appears to disrupt the enhancement associated with spatial attention. Therefore, we have chosen to call the effect a disruption.

Spatial and Feature-Based Attention in V4

Previous neurophysiological studies in area V4 have shown that the effect of spatial attention diminishes during the transient response (Mehta et al., 2000; Reynolds et al., 1999). Two theories have been advanced to explain this finding (Treue, 2001). First, response saturation might limit the efficacy of spatial attention when a neuron is driven to near its maximal firing rate, as often occurs during the response transient. Our data suggest that response saturation is not an important factor in spatial attention.

The second theory is that changes in the magnitude of spatial attention actually reflect a delay in the deployment of spatial attention (Treue, 2001; Lamme and Roelfsema, 2000). This could occur if the early portion of a response reflects a rapid feedforward signal reflecting the visual stimulus, while the sustained portion of the response also reflects the effects of attention (Bisley et al., 2004; Treue, 2001). However, delayed feedback should affect both spatial and feature-based attention, and we find no modulation of feature-based attention over time.

Relationship to Psychophysical Observations

Psychophysical studies suggest that spatial attention is mediated both by top-down and bottom-up processes (Egeth and Yantis, 1997). The top-down process is under volitional control in the service of a specific goal, while the bottom-up process is stimulus driven (Nakayama and Mackeben, 1989). When a new stimulus appears abruptly in the visual field, psychophysical detection thresholds are reduced briefly at its location (Cheal and Lyon, 1991; Egeth and Yantis, 1997; Nakayama and Mackeben, 1989). The disruption peaks about 100–150 ms after stimulus onset and disappears by 250 ms. Our data are roughly consistent with these psychophysical observations, indicating that V4 participates in both the top-down and bottom-up processes.

Spatial and Feature-Based Attention and Natural Vision

The finding that spatial and feature-based attention are controlled in part by different mechanisms may reflect their differing roles during natural vision. The system controlling spatial attention appears to be closely related to the saccade generation system (Moore and Armstrong, 2003; Corbetta et al., 1998; Kustov and Robinson, 1996; Mazer and Gallant, 2003; Moore et al., 2003). Because the retinal positions of locations in the visual field change whenever the eyes move, spatial attention must be updated with every saccade. How does the attentional system know when it is time to update? The reset signal may be a top-down signal, such as a copy of the motor command, or the visual transient associated with the saccade may provide a bottom-up signal to reset spatial attention. The brief disruption of spatial attention that we observe may be a signature of this bottom-up reset process.

Feature-based attention is used to select stimuli that share specific attributes with the target. Because feature-based attention operates across the visual field (McAdams and Maunsell, 2000; Treue and Martinez Trujillo, 1999), it is unlikely to be closely linked to the saccade system. On the contrary, if feature-based attention stores an active representation of the target throughout the task (Chelazzi et al., 2001; Motter, 1994), disruption by saccades could be disadvantageous. In sum, our data are consistent with the idea that spatial and feature-based attention play somewhat distinct roles during natural vision: spatial attention is most important for guiding saccades, while feature-based attention is most important for maintaining an internal representation of the target.

Experimental Procedures

Subjects and Physiological Procedures

All animal procedures were approved by oversight committees at the University of California, Berkeley and were consistent with NIH and USDA regulations. Surgical procedures were conducted under anesthesia using sterile techniques (Mazer and Gallant, 2003; Vinje and Gallant, 2002). Extracellular single-neuron recordings were made with epoxy-coated tungsten electrodes (FHC, Bowdoinham, ME) from two awake, behaving macaques (*Macaca mulatta*). Signals were amplified, band-pass filtered, and isolated with a spike sorter (Plexon Instruments, Dallas, TX). Area V4 was located anatomically by exterior cranial landmarks and/or by direct visualization of the lunate sulcus. Recording locations were confirmed by

comparing receptive field properties to those reported previously (Desimone et al., 1985; Gallant et al., 1996; Gattass et al., 1990).

Stimuli were presented on a CRT with a 60 Hz refresh. Eye position was monitored with an infrared eye tracker (500 Hz; Eyelink II, SR Research, Toronto, ON, Canada). Trials during which the subject's eye position deviated more than 0.5° from the fixation spot were excluded from analysis. Fixation locations in the two spatial attention conditions were not significantly different.

Receptive Field Estimation

The boundaries of each classical receptive field (CRF) were first estimated manually using bars, gratings, and non-Cartesian stimuli (Gallant et al., 1996; Mazer and Gallant, 2003). Receptive field size, shape, and location were confirmed by reverse correlation using a dynamic (10 Hz) sequence of white, black, and textured squares flashed randomly in and around the CRF (Mazer and Gallant, 2003). Reliable CRF estimates were typically obtained with 100 s of data (1000 squares) collected in 20 behavioral fixation trials. The CRF profiles estimated using the two methods usually agreed; when they did not the CRF location was estimated by combining measurements from both procedures. CRF diameters ranged from 3° to 8° (median 5.6°), and their centers were located from 5° to 18° (median 10.2°) from the fixation point.

Behavioral Task

The behavioral task is summarized in Figure 1 and in Movie S1. Each animal initiated a trial by grabbing a capacitive touch bar. A fixation spot then appeared; after fixation was acquired, feature and spatial cues appeared for 150–600 ms. The feature cue consisted of a natural image patch (same size as CRF) centered at the fixation point. The spatial cue was a small red line (<1 degree) superimposed on the edge of the feature cue nearest the stream to be attended. For the majority of the cells, the spatial cue only appeared on the first trial in the block. Care was taken to ensure that the cues never encroached upon the CRF. Analyses revealed that the cue did not affect neuronal responses or performance.

Following an 850 ms blank period two stimulus streams appeared: one in the CRF and the second directly opposite from it, in the opposite quadrant. Patches appeared at a constant rate (3.5–4.5 Hz, varying across cells), and there was no blank period between successive stimuli. To receive a reward, animals had to maintain continuous fixation and release the bar within 1 s of the appearance of the target in the attended stream.

The stimuli were circular patches cut out of black and white digital photographs of natural scenes (Corel Corp.). Patches were chosen by an automated algorithm that selected them at random but that favored patches with broad frequency spectra. Each patch was the same size as the CRF, and the outer 10% was blended linearly into the background. Patches were not normalized for contrast or luminance. At the beginning of each day, two target patches were chosen arbitrarily from the set of all patches. They did not differ statistically from the distractors, and they were chosen without regard to neuronal response properties. To avoid any long-term bias, no patch served as a target on more than one day.

Four attention conditions were constructed by crossing two spatial conditions (attend toward the receptive field, attend away from the receptive field) with two feature conditions (search for target A, search for target B). These conditions were run in blocks of ten trials. To facilitate data analysis, stimulus generation and presentation were constrained to ensure that every sequence of patches was shown in each attention condition. Because of the large number of patches shown on each day (see below) and because each sequence was shown only four times, we are confident that animals did not learn the stimulus sequences.

On any given trial as many as 20 distractor patches could appear before the target. To ensure that attention was deployed correctly and reduce the possibility of anticipatory responses, 5%–20% of the distractors were catches. Spatial catches consisted of the cued target appearing at the uncued location; feature catches consisted of the other target patch appearing at the cued location.

Data Analysis

The experiment followed a two-by-two design, in which two conditions of spatial attention were crossed with two conditions of feature-based attention. Therefore, spatial attention was assessed by collapsing across the feature dimension (by combining data acquired under both feature-based attention states), and feature-based attention was assessed by collapsing across the spatial dimension (by combining data acquired under both spatial attention states). In all cases, the dependent variable was the mean neuronal response observed in a window from 50 to 300 ms after the onset of each distractor, averaged over all repetitions of that attention condition. (For feature-based attention, the patch that evoked higher firing when it was the target was designated the more effective target; the other was called the less effective target.)

The main effects of spatial and feature-based attention and their interaction were assessed by means of a two-factor ANOVA on each neuron. To satisfy the homogeneity of variance assumption of ANOVA, mean response rates were square root transformed before analysis. A main effect of spatial attention was observed in 74% of recorded neurons (81 out of 110 cells; $p \leq 0.05$). A main effect of feature attention was observed in 69% of the cells (76 out of 110; $p < 0.05$). Finally, a significant interaction between spatial and feature-based attention was found in 42% of the cells (46 out of 110; $p < 0.05$). Note, however, that the interaction effect was quite small. On average it was only 2% of the mean evoked response, while the average effect of spatial attention was about 20% of the mean response, and the average effect of feature-based attention was about 10% of the mean response. Because the interaction between spatial and feature-based attention is small in magnitude and is not directly relevant to this paper, it was not pursued further.

PSTHs were calculated for each attention condition separately, by triggering at the onset of each distractor patch and averaging across patches. Responses evoked by the cue, target, and catch stimuli were excluded. The number of individual responses per cell ranged from 48 to 1890 unique patches (median 450) per attention condition.

To measure the change in attentional modulation over time, we assessed the average response evoked during the early and late portions of the response for each neuron. First, the transient peak was identified by searching for an early maximum in the PSTH calculated across all distractors in all attention conditions. Next, PSTHs were obtained to all distractors within each attention condition. Finally, the period from 25 ms before to 25 ms after the transient peak was taken as the early response. The difference between the early responses obtained across the two spatial or two feature-based attention conditions was taken as the early modulation. Late responses were defined as the response within a 50 ms bin beginning 100 ms after the beginning of the early response. The difference between the late responses obtained across the two spatial or two feature-based attention conditions was taken as the late modulation. Attentional disruption was measured by subtracting the late modulation from the early modulation separately for spatial and feature-based attention conditions.

A two-tailed randomized t test was used to assess whether attentional modulation of the early and late portions of the visual response were significantly different (Vinje and Gallant, 2002). The distribution expected by chance was determined by randomly permuting measured modulations between early and late conditions 1000 times. An effect was accepted as significant if the observed modulation was greater than 97.5% or smaller than 2.5% or of the randomized distribution ($p < 0.05$).

In order to ensure that the results were not an artifact of the time windows used to define early and late responses, the entire procedure was repeated using several binning schemes. Early modulation was estimated using bins of 16 ms, 32 ms, and 64 ms; late modulation used bins of 16 ms, 32 ms, 64 ms, and 100 ms and delays of 80, 120, and 150 ms. In all cases, results were qualitatively similar to those reported here.

In one control analysis, PSTHs were recalculated using subsets of distractor patches. To determine which patches to analyze, the response to the distractors was computed. The response was quantified as the average number of spikes evoked in all four attention conditions in the window from 50 to 300 ms after the image appeared. Neurons for which one target evoked higher firing than the average response to all distractors and the other target evoked lower firing than the average response to all distractors were extracted. Target response was computed by averaging the response

to the target in any condition in which it appeared. For the control analyses, PSTHs were recomputed using the subset of distractors and the subset of neurons.

Supplemental Data

The Supplemental Data include one movie and can be found with this article online at http://www.neuron.org/cgi/content/full/47/5/637/DC1/.

Acknowledgments

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References

Bisley, J.W., Krishna, B.S., and Goldberg, M.E. (2004). A rapid and precise on-response in posterior parietal cortex. J. Neurosci. *24*, 1833–1838.

Bundesen, C. (1990). A theory of visual attention. Psychol. Rev. *97*, 523–547.

Cheal, M., and Lyon, D.R. (1991). Central and peripheral precuing of forced-choice discrimination. Q. J. Exp. Psychol. A *43*, 859–880.

Chelazzi, L., Miller, E.K., Duncan, J., and Desimone, R. (2001). Responses of neurons in macaque area V4 during memory-guided visual search. Cereb. Cortex *11*, 761–772.

Corbetta, M., Akbudak, E., Conturo, T.E., Snyder, A.Z., Ollinger, J.M., Drury, H.A., Linenweber, M.R., Petersen, S.E., Raichle, M.E., Van Essen, D.C., and Shulman, G.L. (1998). A common network of functional areas for attention and eye movements. Neuron *21*, 761–773.

David, S.V., Vinje, W.E., and Gallant, J.L. (2004). Natural stimulus statistics alter the receptive field structure of V1 neurons. J. Neurosci. *24*, 6991–7006.

Dean, A.F., Tolhurst, D.J., and Walker, N.S. (1982). Non-linear temporal summation by simple cells in cat striate cortex demonstrated by failure of superposition. Exp. Brain Res. *45*, 456–458.

Desimone, R., and Duncan, J. (1995). Neural mechanisms of selective visual attention. Annu. Rev. Neurosci. *18*, 193–222.

Desimone, R., Schein, S.J., Moran, J., and Ungerleider, L.G. (1985). Contour, color and shape analysis beyond the striate cortex. Vision Res. *25*, 441–452.

De Valois, R.L., and De Valois, K.K. (1990). Spatial Vision, Volume 14 (Oxford: Oxford University Press).

Egeth, H.E., and Yantis, S. (1997). Visual attention: control, representation, and time course. Annu. Rev. Psychol. *48*, 269–297.

Gallant, J.L., Connor, C.E., Rakshit, S., Lewis, J.W., and Van Essen, D.C. (1996). Neural responses to polar, hyperbolic, and Cartesian gratings in area V4 of the macaque monkey. J. Neurophysiol. *76*, 2718–2739.

Gattass, R., Rosa, M.G., Sousa, A.P., Pinon, M.C., Fiorani Junior, M., and Neuenschwander, S. (1990). Cortical streams of visual information processing in primates. Braz. J. Med. Biol. Res. *23*, 375–393.

Kustov, A.A., and Robinson, D.L. (1996). Shared neural control of attentional shifts and eye movements. Nature *384*, 74–77.

Lamme, V.A., and Roelfsema, P.R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. Trends Neurosci. *23*, 571–579.

Lamy, D., and Tsal, Y. (2001). On the status of location in visual attention. Eur. J. Cogn. Psychol. *13*, 305–342.

Maljkovic, V., and Nakayama, K. (1996). Priming of pop-out: II. The role of position. Percept. Psychophys. *58*, 977–991.

Mazer, J.A., and Gallant, J.L. (2003). Goal-related activity in V4 during free viewing visual search. Evidence for a ventral stream visual salience map. Neuron *40*, 1241–1250.

McAdams, C.J., and Maunsell, J.H. (1999). Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4. J. Neurosci. *19*, 431–441.

McAdams, C.J., and Maunsell, J.H. (2000). Attention to both space and feature modulates neuronal responses in macaque area V4. J. Neurophysiol. *83*, 1751–1755.

Mehta, A.D., Ulbert, I., and Schroeder, C.E. (2000). Intermodal selective attention in monkeys. I: distribution and timing of effects across visual areas. Cereb. Cortex *10*, 343–358.

Moore, T., and Armstrong, K.M. (2003). Selective gating of visual signals by microstimulation of frontal cortex. Nature *421*, 370–373.

Moore, T., Armstrong, K.M., and Fallah, M. (2003). Visuomotor origins of covert spatial attention. Neuron *40*, 671–683.

Motter, B.C. (1994). Neural correlates of attentive selection for color or luminance in extrastriate area V4. J. Neurosci. *14*, 2178–2189.

Nakayama, K., and Mackeben, M. (1989). Sustained and transient components of focal visual attention. Vision Res. *29*, 1631–1647.

Reynolds, J.H., and Chelazzi, L. (2004). Attentional modulation of visual processing. Annu. Rev. Neurosci. *27*, 611–647.

Reynolds, J.H., Chelazzi, L., and Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. J. Neurosci. *19*, 1736–1753.

Shih, S.I., and Sperling, G. (1996). Is there feature-based attentional selection in visual search? J. Exp. Psychol. Hum. Percept. Perform. *22*, 758–779.

Tanaka, K. (1996). Inferotemporal cortex and object vision. Annu. Rev. Neurosci. *19*, 109–139.

Treue, S. (2001). Neural correlates of attention in primate visual cortex. Trends Neurosci. *24*, 295–300.

Treue, S., and Martinez Trujillo, J.C. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. Nature *399*, 575–579.

Tsal, Y., and Lavie, N. (1993). Location dominance in attending to color and shape. J. Exp. Psychol. Hum. Percept. Perform. *19*, 131–139.

Vinje, W.E., and Gallant, J.L. (2002). Natural stimulation of the nonclassical receptive field increases information transmission efficiency in V1. J. Neurosci. *22*, 2904–2915.