

Supporting Information

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SI Text

Supporting Results. Behavioral data. Both human and macaque behavioral data on the search for conjunctions of color and direction-of-motion features have been published previously (1). For convenience herein, we present key facts. As reported previously by Nakayama and Silverman (2), human performance exhibited search array size-independent search times for feature search and linearly increasing search times with set size for conjunction search, and error rates remained low (<5%). This pattern of performance is consistent with a serial search strategy whereby error incidence is minimized.

Fig. S1 summarizes macaque performance for feature and conjunction search. Macaque performance followed a comparable pattern, albeit with a bias toward speed in the speed-accuracy tradeoff. Five monkeys were trained to perform the search tasks. Feature and conjunction search tasks were performed by using search arrays of size 2, 4, and 8 items (note that search arrays for training were somewhat different from those used for single unit recording in that they consisted of randomized sets of apertures; see ref. 1 for details).

Pooling modulation indices across target-in-RF and antitarget-in-RF conditions. Both experiments I and II include stimulus/task conditions that are comparable (i.e., conditions I.1, II.1 and I.3, II.3), and thus the corresponding data are amenable to pooling. We first present modulation index statistics for 53 neurons recorded in experiment II. For target-in-RF conditions of experiment II (condition II.1), we found that in the motion-cueing case median MI was 23% (mean MI = 40%; $n = 46$, U test $P < 10^{-5}$), and in color-cueing case median MI was 20% (mean 66%, $n = 50$, U test $P < 10^{-5}$). For antitarget-in-RF conditions (II.3) in the case of motion cueing median MI was 2% (mean MI = 11%; $n = 42$, U test $P = 0.24$), and in the case of color cueing median MI was 2% (mean 22%, $n = 37$, U test $P = 0.72$). Wilcoxon–Mann–Whitney tests comparing MI distributions for motion-cueing and color-cueing cases for target-in-RF ($P = 0.9$) and antitarget-in-RF ($P = 0.59$) conditions did not reveal any differences. We did not observe correlation between MIs for color-cueing vs. motion-cueing cases either (target-in-RF condition: correlation coefficient = 0.02, $P = 0.55$). These comparison results justify pooling MIs across motion-cueing and color-cueing conditions.

Next, we compared the distributions of modulation indices for corresponding conditions of experiments I and II. Thus MI distributions for 18 neurons of experiment I were compared with MI distributions of 53 neurons of Experiment II using the nonparametric Wilcoxon–Mann–Whitney rank-sum test for testing whether two samples came from the same distribution. There were no differences in MI distributions for target-in-RF conditions (motion-cueing: $P = 0.5$; color-cueing: $P = 0.48$) and for antitarget-in-RF conditions (motion-cueing: $P = 0.8$; color-cueing: $P = 0.81$).

Because we did not find differences between MI distributions for experiments I and II, we pooled data across these experiments. The statistics of the pooled data are presented in the main text.

End-point modulation onset times. Is the end-stage modulation a genuinely spatially-selective phenomenon or a superposition of feature-specific (color- and motion-specific) effects? To address this possibility, we examined the distribution of modulation onset times relative to saccade onset for conditions I.1 and II.2 (see Fig. S2). Feature-specific gain modulations in primate visual cortex have been shown to be locked to stimulus onset and manifested as early as 90–120 ms after stimulus onset, and hence

covary with saccade latency (3). Contrary to this prediction, we found that modulation onset times were not correlated with end-stage modulation onset times ($r = 0.14$; $P > 0.05$), and onset times were clustered within the interval of 50–120 ms before the saccade. Thus, the end-stage modulation dynamics are consistent with the hypothesis that response modulation is a neural correlate of spatial attentional selection, which leads to target identification.

Correlations between modulation during error trials and behavioral performance. Next, we addressed the possibility that the reduced modulation strength during error-to-RF trials was a result of reduced alertness. Assuming that behavioral performance level reflects alertness during a given recording session, we calculated the correlation between behavioral performance during each single-unit recording session and associated end-stage modulation strength. No correlation was observed (correlation coefficient = 0.09, $P = 0.7$, $n = 42$). Thus, it is unlikely that the difference in modulation indices between correct and error-to-RF trials is a manifestation of variations in alertness from one session to another.

Supporting Discussion. Attentional facilitation. Behaviorally, attentional facilitation refers to the improved sensitivity of an observer to a stimulus that appears at an attended location. Neuronal facilitatory effects refer to corresponding increases in firing rate elicited by a stimulus when it appears at an attended location. Such effects have been observed in a number of different brain regions, including posterior parietal cortex (e.g., refs. 4–6) area V4 (7, 8), and area MT (9). fMRI studies of attention have revealed attentional modulations in areas V1, V2, V3, V3A (10–12) of human visual system and as early as LGN (13). These effects are believed to underlie improved behavioral sensitivity.

The results reported herein resemble previously reported facilitatory effects. There exists, however, at least one key difference: The response enhancement seen in the studies cited above was associated with a stimulus event (e.g., stimulus onset). By contrast, the response modulation observed in experiment I was more closely linked to the behavioral index of target identification. This distinction may simply reflect the output of a common attentional gain control mechanism in the face of different behavioral requirements. Nonetheless, the dissociation between stimulus events and response modulation that we have observed adds critical weight to the claim that the modulation does indeed reflect a shift of spatial attention.

Do response modulations in MT reflect motor preparation? Because the modulations we have observed were associated with saccadic eye movements, we must consider the possibility that they reflected “motor preparation” rather than attention. Empirical arguments against this hypothesis come from the findings in experiment II that (i) response modulation often depended on the specific configuration of the search display and (ii) RF-directed saccades on error trials (i.e., when the RF stimulus was not a target) yielded dramatically reduced presaccadic response modulation. A related study by Bichot et al. (14) also found potent modulations in area V4 that were not followed by foveation of the RF and thus cannot be readily explained by the motor preparation hypothesis.

Stimulus-dependence of end-stage modulations. We were surprised to find in experiment II that response modulations elicited using motion-cueing search arrays were sometimes different in magnitude from those elicited using color-cueing search arrays

(compare the two top rows of Fig. 4). We hypothesize that the cue-specific modulation stems from differential engagement of RF surrounds. Motion-cueing search arrays were configured such that stimuli adjacent to the RF contained motion in the direction opposite to that of the RF stimulus. Conversely, color-cueing search arrays were configured such that stimuli adjacent to the RF contained motion in the same direction as the RF stimulus. Preference for center-surround motion contrast vs. wide-field motion has been used to define cell types in area MT (15). Furthermore, attention tends to modulate responses to stimuli that do not saturate neuronal activity when unattended (e.g., ref. 16). We thus speculate that the magnitude of response modulations was cue-specific only for neurons for which the presence or absence of center-surround contrast in one cue condition resulted in a suboptimal response.

Comparison with the study of Bichot et al. Bichot et al. (14) reported a potent end-stage-of-search modulation similar to the effect reported herein. Interestingly, these investigators also reported a strong modulation (median increase in firing rate by 30%) present during the feature-search task when a stimulus sharing a feature with the target was brought into the RF. This modulation was interpreted as a manifestation of purely feature-specific effect. The search array used in this task, however, contained only one item that possessed the cued feature, which was the target. There is thus a possibility that the observed modulations were associated not only with featural but also spatial attention. Indeed the dynamics of this modulation did not differ from the dynamics of the end-stage modulation (Fig. 2*A* and *B* and figure 5*A* of ref. 14). This possibility is further supported by the fact that feature-specific modulation measured during the color-shape conjunction search task was significantly weaker than that reported for the feature search task. This finding is in line with our observations of feature-specific effects in area MT. Finally, these authors addressed search-related modulations associated with features (shape, color) in an area (V4) that actually represents those features. By contrast, our study addresses not only a feature represented in the area under study (direction of motion in area MT), but also cross-dimensional feature specific effects (MT neurons are known not to discriminate among isoluminant colors).

Supporting Methods. Visual stimulus presentation and eye tracking.

Stimuli were displayed on a 19-in video monitor (60Hz noninterlaced; Phillips). The voltage/luminance relationship was linearized independently for each of the three guns in the display (17, 18). Stimulus movement was achieved by updating the frame buffer in synchrony with the vertical refresh of the video monitor. The computer also controlled behavioral data acquisition and monitored eye position. Monkeys were seated in a standard primate chair and viewed the display from a distance of 60 cm. Head movements were prevented by bolting the head post to the chair frame. Eye position was monitored continuously by using a scleral search coil (19). A trial was aborted immediately if eye position deviated from a 1° square window centered on the fixation spot at any time before the appearance of the search array.

Experimental design. For experiment I, the color and direction (preferred vs. nonpreferred) of the RF stimulus were explicitly determined by the experimental condition, as described above. Color and motion values for the remaining seven distractors were assigned pseudorandomly and differently for each recorded cell. The following constraints were used when assigning distractor feature values: (i) For all conditions and trials, both directions were present in equal numbers, but due to the rule of having only one target per array, stimulus colors were distributed so that there were five stimuli of the cued color and the remaining three were of the nontarget color during target-present trials. During target-absent trials the target combination feature was missing and the remaining three combinations were

distributed pseudorandomly over the eight stimuli. (ii) For all conditions, the colors of all search stimuli were switched randomly but congruently on different trials, so that each stimulus was red or green with equal frequency while preserving the color and motion distribution pattern.

(iii) Assigned directions of search stimuli neighboring RF (two on each side) were identical across all preferred-in-RF conditions. (iv) Assigned directions of stimuli neighboring RF were identical across all anti-preferred-in-RF conditions. (v) Directions of the remaining (non-RF and nonneighboring) search stimuli were randomized across all conditions. These rules yielded search array configurations that were sufficiently diverse across trials as to engage genuine visual search (1). They also insured that the directional contrast between the RF and neighboring regions of visual space was constant for all three preferred-in-RF and all three antipreferred-in-RF conditions, so that potential nonclassical RF effects were identical for all conditions. All conditions were randomly interleaved within a recording session.

In experiment II, the four conditions for each cueing type (color- and motion-cueing conditions, see Table 1) differed primarily with respect to the cue that preceded the search array. The two sets of conditions differed from one another in two ways:

(i) The definition of semitargets differed. Under color-cueing conditions, semitargets were search stimuli sharing the target color but not its motion. Under motion-cueing conditions, semitargets shared target motion but not its color. This distinction was only manifested as a difference in the way data were parsed and analyzed.

(ii) The search arrays differed with respect to the attributes of the stimuli proximal to the RF stimulus: the RF stimulus was always distinguished from surrounding stimuli by contrast along one feature dimension. Thus, in motion-cueing conditions, the proximal stimuli contained motions in the direction opposite that of the RF stimulus and colors identical to the RF stimulus, so that salience of the RF stimulus was enhanced solely by motion contrast (see Fig. 3*A*). In color-cueing conditions, the proximal stimuli contained colors different from the RF stimulus, which enhanced RF stimulus saliency by color contrast (see Fig. 4*A*). Because of these differences across the two sets of conditions, cross-condition analysis was restricted to within-set comparisons.

A more detailed account on the search array design for experiment II is presented below. Feature values in search arrays designed for testing feature-specific effects were distributed in the following way. To prevent contribution of stimulus differences in the receptive field surround across various experimental conditions we designed a set of minimum-difference search arrays: The search array area was partitioned into two sides: ipsi- and contrareceptive field (Fig. S3). Every circle in Fig. S3 represents a search array. The light-gray half circle shows stimuli ipsilateral to the receptive field, and the dark-gray shows contralateral stimuli. The stimuli on the ipsi-side assumed the same motion direction values for all experimental conditions. Color of the stimuli on the ipsi-side was randomly globally inverted depending on the target color (e.g., all previously red apertures would assume green, and all green apertures would assume a red color). Note that antitarget-in-RF condition used a search array that was identical in all respects to the search array of the target-in-RF condition. The difference between these conditions was only in the sample features: in one case the sample assumed the feature values of the search-array aperture inside a RF (hence target-in-RF condition), whereas in the other case, the sample assumed the feature values of a search-array aperture outside the RF. In all our search arrays only direction of motion within the contralateral apertures could be modified from one trial to another, and the ipsireceptive-field apertures were held

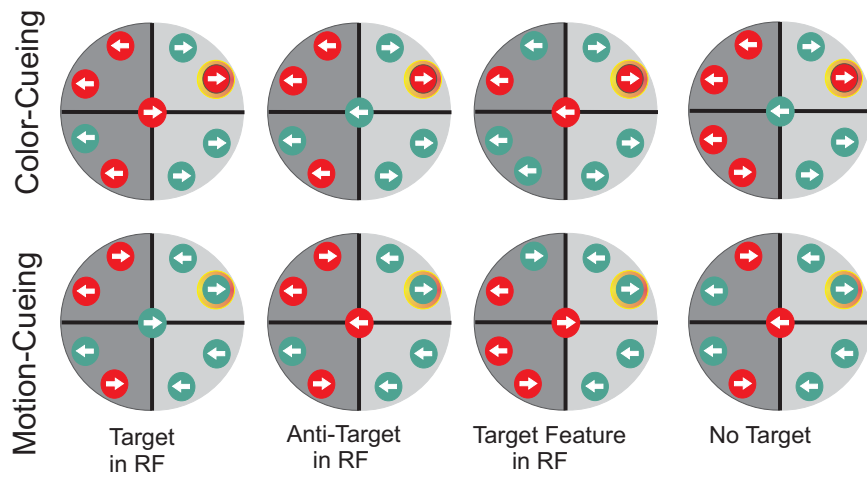


Fig. S3. Neuronal modulation onset times are uncorrelated with behavioral response (saccade) latencies. Neuronal modulation onset times were measured relative to saccade initiation. Behavioral response latencies were measured relative to appearance of the visual search display. Each data point represents MI and modulation onset times for one cell. The line represents the least-squares fit to the data. The two variables were not significantly correlated ($r = 0.14$). Marginal distributions independently convey behavioral latencies (vertical histogram) and neuronal modulation onset times (horizontal histogram). Arrows indicate median values for each distribution. Clustering of modulation onset times ≈ 100 ms prior to saccade suggests an association with the behavioral response rather than the appearance of the search display.