Effects of similarity and history on neural mechanisms of visual selection

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To investigate how the brain combines knowledge with visual processing to locate eye movement targets, we trained monkeys to search for a target defined by a conjunction of color and shape. On successful trials, neurons in the frontal eye field not only discriminated the target from distractors, but also discriminated distractors that shared a target feature as well as distractors that had been the search target during the previous session. Likewise, occasional errant saccades tended to direct gaze to distractors that either resembled the current target or had been the previous target. These findings show that the frontal eye field is involved in visual and not just motor selection and that visual selection is influenced by long-term priming. The data support the hypothesis that visual selection can be accomplished by parallel processing of objects based on their elementary features.

Gaze is commonly attracted to conspicuous stimuli. We have previously investigated neural correlates of effortless, 'popout' visual search using displays in which the target was distinguished from distractors by a unique feature (for example, a red item among green items)[1]. The frontal eye field (FEF) is central for transforming the outcome of visual processing into a command to orient[2] by virtue of extensive connections with visual areas of both the dorsal and ventral streams[3,4], as well as connections with subcortical oculomotor structures[5,6]. The initial activity of visually responsive neurons in FEF did not discriminate whether the target or only distractors of the search array appeared in their receptive field[7]. This absence of early discrimination is not surprising because FEF neurons are not selective for stimulus properties such as color and orientation[8]. However, before a saccade was made to fixate the target, the activity of FEF neurons evolved to signal the location of the target through attenuation of the activity evoked by distractors.

Gaze is also guided by experience and knowledge[9]. During popout search, repetition of the target and distractor properties across trials improves performance of humans[10], as well as monkeys[11]. Sometimes, knowledge can even override conspicuousness. Monkeys trained exclusively with a target and distractors of fixed colors during popout search, when presented with a search array with the target and distractor colors reversed, ignore the salient target and shift gaze to distractors of the learned target color[12]. We have found that, under these circumstances, visual selectivity in FEF is dramatically altered; half of the neurons now discriminate the target from distractors in their initial visual response.

When objects are defined by combinations of features, knowledge and vision must collaborate to guide gaze because memory is required to locate an object with particular features. To understand neural mechanisms of visual selection when knowledge is required to locate the target, we trained monkeys to perform a conjunction visual search (Fig. 1b), a task that has been critical in the development of theories of visual search and attention. For this experiment, the target was specified as one combination of color and shape, and distractors were formed by other possible combinations. Thus, the target cannot be distinguished from the distractors on any given dimension, but must be located by comparing the unique combination of features to a memory representation.

Early experiments[13] reported a clear dichotomy between popout search and conjunction search. Whereas the time to find the target was not affected by the number of distractors during popout search, it became significantly longer during conjunction search with increasing number of distractors. This finding, among others, was interpreted as evidence that the search process in conjunction search was serial, although the same results can be produced by limited-capacity parallel search mechanisms[14]. Moreover, subsequent experiments showed that some conjunction searches can be performed efficiently, as reflected by smaller effects of the number of distractors on target detection[15–17]. These findings led to the development of models of visual search in which selection is guided by the similarity between the target and distractors[18], most likely through parallel processing of the individual features that define the conjunction stimuli as in the guided-search model[19,20] or the revised feature integration theory of visual search[21].

We have found that monkeys can perform conjunction searches as efficiently as humans based on reaction time measures. Furthermore, when monkeys fail to fixate the target during conjunction search, in addition to exhibiting a tendency to shift gaze to distractors that had been the target during the previous session, they are significantly more likely to shift gaze to a distractor that shares a target feature than to a distractor that shares none[11], similar to humans[22,23]. The influence on gaze shifts of visual similarity to the target is consistent with measurements of attentional allocation at stimulus locations during conjunction search[24], which should not be surprising considering the growing evidence for a strong link between eye movements and atten-

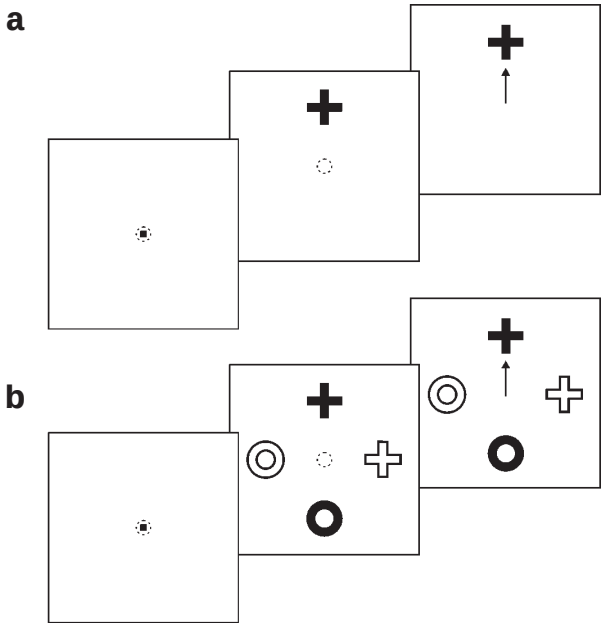

Fig. 1. Behavioral tasks. The monkeys' task was to shift gaze to a target defined by a conjunction of shape and color during detection trials in which the target was presented alone **(a)** and conjunction search trials in which the target was presented along with distractors **(b)**. Detection trials defined the target, which did not change within a daily experimental session. Dotted circles represent the monkey's current point of fixation; the arrow represents the saccade to the target. Stimuli are not drawn to scale.

tion[25–28]. Altogether, these results support models of visual search in which selection during conjunction search is guided by the similarity among stimuli.

Ultimately, behavioral studies provide only inferential conclusions, and the combination of behavioral and neurophysiological data is necessary for understanding the architecture of human cognition[29]. Therefore, we tested whether a neural correlate of visual selection in FEF was influenced by visual similarity and by the history of target properties in a manner that would explain the pattern of errors during conjunction search and thus provide insight into mechanisms of visual selection. These data also address the question of whether the selection observed in FEF is related to visual processing or motor preparation.

Results

Initial detection trials in which the target was presented alone were used to map the receptive field of neurons (Fig. 1a). Conjunction search arrays were configured such that one stimulus always fell in the most sensitive part of the receptive field. Detection trials also instructed monkeys what combination of color and shape would be the target for the session. To prevent strong learning effects[12], the target for each session was defined by a combination of color and shape different from that used in the previous session. We recorded 62 neurons in 49 penetrations from the FEF of two monkeys, of which 53 provided sufficient data for the analyses presented here. Across the data, the target was the same color as the target in the previous session during recordings from 19 neurons, it was the same shape during recordings from 16 neurons, and it differed in both color and shape during recordings from 18 neurons. Recording sessions were usually conducted on successive days, with no significant difference in the average delay between sessions in which the target changed in color, shape or both features.

Overall, monkeys made errors in 7% and 12% of trials with 4- and 6-stimulus displays, respectively. Of these errors, 86% and 88%, respectively, were saccades to one of the distractors. During recordings from each neuron, we measured the incidence of saccades to the three types of distractors, which accounts for the different numbers of distractor types within and across display sizes. We first computed the percentage of saccades made to each distractor type in trials in which an initial saccade was made to a distractor. The percentages obtained for each distractor type were divided by the number of distractors of that type in the display and then normalized so that the sum of the percentages for the three distractor types would equal 100% (Fig. 2). During neural recordings, monkeys made saccades to distractors that shared a target feature (that is, same-color or same-shape distractors) significantly more often than they made saccades to a distractor that did not (opposite distractor). In addition, the history of target properties across sessions affected performance, as shown by an increased tendency to make saccades to a distractor that had been the target during the previous session. This effect may be a form of priming[10,30], so we will refer to a distractor with such a bias as the 'primed' distractor. The effects of visual similarity and priming on the incidence of saccades to the three distractor types observed during neural recordings in this study replicated the observations made in our previous behavioral study[11].

The initial visual response of two FEF neurons during conjunction search trials in which the initial saccade was directed to the target (Fig. 3) was the same regardless of what feature conjunction appeared in the receptive field, but over time the activity evolved to discriminate the target from distractors in the receptive field. This report focuses on the differential activation elicited by the various distractor types after discrimination occurred but before initiation of the correct saccade to the target. The physiology associated with errant saccades will be the focus of a future report. We observed two influences on neurons. First, for both neurons, the activity was greater when the distractor in the receptive field was the same color or shape as the target than when it shared no feature with the target. Second, the activity of the neurons was relatively greater when the distractor

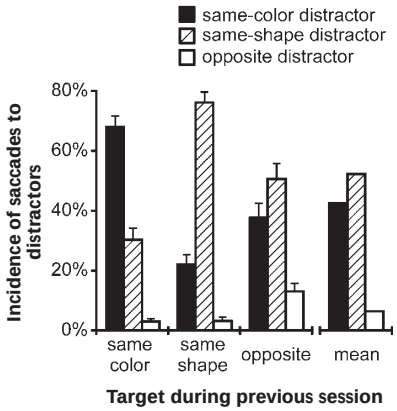

Fig. 2. Gaze pattern in conjunction search during neural recordings. Incidence of saccades to distractors having the same color (black) or the same shape (striped) as the target, or having features opposite to the target (unfilled) is shown as a function of the target properties in the previous session. Error bars, s.e.

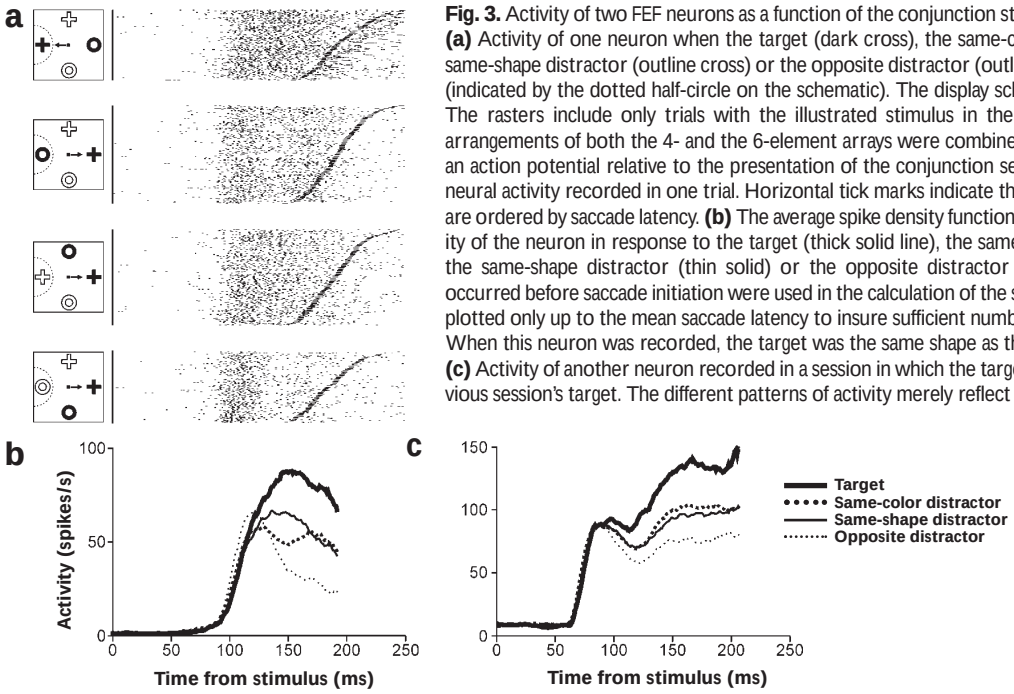

Fig. 3. Activity of two FEF neurons as a function of the conjunction stimulus type in the receptive field. **(a)** Activity of one neuron when the target (dark cross), the same-color distractor (dark circle), the same-shape distractor (outline cross) or the opposite distractor (outline circle) fell in its receptive field (indicated by the dotted half-circle on the schematic). The display schematics are for illustration only. The rasters include only trials with the illustrated stimulus in the receptive field, but all possible arrangements of both the 4- and the 6-element arrays were combined. Each dot indicates the time of an action potential relative to the presentation of the conjunction search array; each row represents neural activity recorded in one trial. Horizontal tick marks indicate the time of saccade initiation; trials are ordered by saccade latency. **(b)** The average spike density functions are superimposed for the activity of the neuron in response to the target (thick solid line), the same-color distractor (thick dotted), the same-shape distractor (thin solid) or the opposite distractor (thin dotted). Only spikes that occurred before saccade initiation were used in the calculation of the spike density functions, which are plotted only up to the mean saccade latency to insure sufficient number of trials for reliable measures. When this neuron was recorded, the target was the same shape as the target of the previous session. **(c)** Activity of another neuron recorded in a session in which the target was the same color as the previous session's target. The different patterns of activity merely reflect the variability in FEF neurons.

that had been the target during the previous session was in the receptive field than when other distractors were in the receptive field. The effect of target history on distractor discrimination was observed when the target for the current session was the same shape (Fig. 3a and b) as well as when it was the same color (Fig. 3c) as the target in the previous session. Note that the priming effect dissipated over time within a trial for these neurons. That is, close to saccade initiation, the difference was reduced between the neural representations of the primed and unprimed distractors that share target features.

To quantify the effects of visual similarity and priming on visual processing in FEF, we measured average neural activity (based on spike count) associated with the three types of distractors in a 30-millisecond interval immediately following the time at which a neuron first discriminated the target from distractors. To compare the level of activity when different types of distractors fell in the receptive field, for each neuron, we calculated pairwise differences between the average activity when each type of distractor fell in the receptive field. Because of the variable firing rates across the population of neurons, the pairwise differences were normalized by dividing by the average of the activity for all three distractor types. Because of differences in the numbers of each distractor type in 4- and 6-item displays, and because saccade latency increases slightly with set size[11,17], all analyses were conducted separately for the two set sizes. However, there were no significant differences in the pattern of neural modulation between the two set sizes, so the data were combined.

Regardless of how target features changed between consecutive sessions, the neural representation of a distractor that shared a target feature was stronger than the representation of a distractor that shared no target feature. Specifically, the activity when a distractor with the same color as the target fell in the receptive field was significantly greater than the activity when a distractor with features opposite the target fell in the receptive field. This was the case whether the target during the previous session was the same-color distractor (Fig. 4a), the same-shape distractor (Fig. 4d) or the opposite distractor (Fig. 4g) in the current session. The same relationships were found when a distractor with the same shape as the target fell in the receptive field (Fig. 4b, e and h).

Priming derived from the history of the targets used across sessions resulted in an increased neural representation of the distractors that had been the target during the previous session. Several analyses support this conclusion. When the target remained the same color across consecutive sessions, the activity representing the primed same-color distractor was significantly greater than the activity representing the unprimed same-shape distractor (Fig. 4c). In addition, the difference between the activity representing the primed same-color distractor and the activity representing the opposite distractor (Fig. 4a) was greater than the difference when neither was primed (Fig. 4d; *t*-test: $t_{68} = 3.1$, $p < 0.01$). Likewise, when the target remained the same shape across consecutive sessions, the activity representing the primed same-shape distractor was significantly greater than the activity representing the unprimed same-color distractor (Fig. 4f), and the difference between the activity representing the primed same-shape distractor and the activity representing the opposite distractor (Fig. 4e) was significantly greater than the difference when neither was primed (Fig. 4b; $t_{68} = 2.2$, $p < 0.05$). Finally, when the target changed in both color and shape, the difference between the representation of a distractor that shared a target feature and the activity representing the primed opposite distractor was significantly smaller than the corresponding difference when neither the distractor similar to the target nor the opposite distractor was primed (compare Fig. 4g and h with d and b; $t_{140} = 2.6$, $p < 0.01$).

Color and shape information contributed equally to locating the target for the stimuli we used. The same-color and same-shape distractor representations were not significantly different when neither distractor was primed (Fig. 4i). Furthermore, the magnitude of the difference between same-color and same-

shape distractor representations did not depend on which was primed (compare Fig. 4c and f; $t_{68} = 0.50$, $p = 0.62$).

As mentioned, the degree of neural selectivity varied over time within a trial. To assess the evolution of the selection processes, we conducted the same series of analyses during the interval from 40 to 10 milliseconds before the initiation of the saccade. This interval extended until 10 milliseconds before saccade initiation because several physiological findings suggest that FEF cannot influence saccade initiation later than this time[31,32]. Visual similarity still influenced neural selection. The representation of the same-color distractor was significantly greater than the representation of the opposite distractor when neither was primed (mean normalized difference, 0.21; $t_{31} = 5.4$, $p < 0.001$); the same was true of the same-shape distractor compared to the opposite distractor (mean normalized difference, 0.30; $t_{37} = 4.7$, $p < 0.001$). In contrast, priming had a reduced effect on the selection process immediately before saccade initiation. Although there was an overall effect of priming on the neural representation of distractors similar to the target (mean increase due to priming in the normalized difference between distractors similar to the target and the opposite distractor, 0.14; $t_{138} = 2.17$, $p < 0.05$), this effect was not significant when measured on same-color and same-shape distractors separately ($t_{68} = 1.9$, $p = 0.07$ and $t_{68} = 1.4$, $p = 0.18$). Nevertheless, the difference between the neural representations of a distractor similar to the target and the opposite distractor was still significantly smaller when the opposite distractor was primed ($t_{140} = 3.9$, $p < 0.001$).

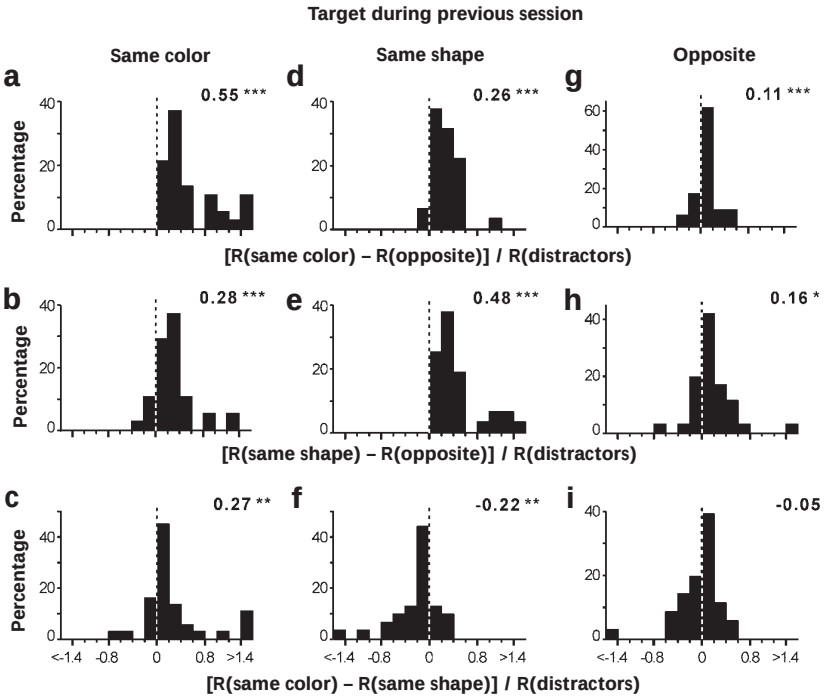

Fig. 4. Feature-based selection and long-term priming in FEF during conjunction search. Distributions of normalized differences between the activity when same-color versus opposite distractors fell in the receptive field when the target during the previous session was the same-color distractor **(a)**, the same-shape distractor **(d)** and the opposite distractor **(g)**. Distributions of normalized differences between the activity for same-shape and opposite distractors **(b, e, h)** and between the activity for same-color and same-shape distractors **(c, f, i)** for the same conditions. The mean of each distribution is indicated in each plot. The two-tailed probability, based on a *t*-test, that the mean of each distribution is significantly different from zero is indicated $*p < 0.05$; $**p < 0.01$; $***p < 0.001$.

Overall, the patterns of neural activation observed during correct trials in FEF and the patterns of gaze shifts in correct and error trials seem to be the outcome of common search mechanisms. To assess whether the pattern of neural activity representing the different distractors related to behavior, we calculated the correlation between, on one hand, the normalized difference between the representation of a distractor that resembles the target and the representation of the dissimilar distractor (measured in the interval immediately following target discrimination) and, on the other hand, the difference in the incidence of saccades to that similar distractor and the incidence of saccades to the dissimilar distractor during physiological recordings. The correlation between neural modulation and gaze behavior on a neuron-by-neuron basis was highly significant (Pearson's correlation coefficient $r = 0.49$, $p < 0.001$). This correlation between behavior and physiology is especially informative because the behavioral influence of visual similarity and priming were observed in error trials, whereas the physiological effects were assessed in correct trials.

Discussion

In monkeys trained to perform a conjunction visual search task comparable to cognitive psychology experiments, we have shown the effect of visual similarity and the effect of the history of target properties on neural selection. The neural representation in FEF was stronger for distractors that were similar to the target than for those that were not; likewise, when they made an error, monkeys were more likely to look at a similar distractor than at a dissimilar one. This finding provides the first neurophysiological evidence that efficient selection during conjunction search is achieved based on the similarity between target and distractors, most likely through parallel processing of the individual features that define the visual objects[19–21].

FEF neurons also tended to have an enhanced representation of a distractor that had been the target for search during the previous session; likewise, monkeys tended to look at the primed distractor more often. The neural modulation associated with the history of target properties and the associated pattern of gaze errors manifests the influence of experience on the search process[30], possibly through a form of long-term priming. Behavioral studies with humans[10], as well as nonhuman primates[11], have described effects of perceptual priming with a shorter time course. Repetition of the target and distractor properties across trials during a popout search improved performance, and this priming had a cumulative influence with a time-span of 5–10 trials or approximately 30 seconds. In contrast to the short-term perceptual priming observed during feature search, the priming we observed during conjunction search was revealed across consecutive experimental sessions at least a day apart and persisted throughout the entire session[11].

This experiment also tests whether selection in FEF represents the outcome of visual processing or motor preparation. In our previous studies of popout visual search, the neural discrimination of the target from distractors could be argued to represent motor preparation because a saccade was made into the response field if the target was there, but not if a distractor was there. We have presented evidence arguing against this hypothesis. First, the time at which a majority of FEF neurons discriminate the target from distractors does not predict the variability of reaction time and is instead more related to the time of stimulus presentation[33]. Second, FEF neurons select the oddball of an array even when monkeys withhold saccades[34]. The current study provides additional evidence that FEF participates in visual selection. Even when saccades were directed to the target outside the receptive field, neurons were activated differentially by the distractors in the receptive field as a function of their visual similarity to the target.

Models of visual search have commonly used maps in which elementary stimulus features are processed. These feature maps, in turn, project to a master salience map in which objects are coded for their behavioral relevance in terms of the combination of their features[13,19,35]. Overall, the findings from this and previous studies support the view that FEF encodes a map of the visual field in which stimulus locations are tagged for orienting based on behavioral relevance derived from conspicuousness as well as knowledge or expectancy[36].

Methods

Subjects and physiological procedures. Data were collected from one *Macaca mulatta* and one *Macaca radiata*, weighing 9 and 5 kg, respectively. The animals were cared for in accordance with the National Institute of Health Guide for the Care and Use of Laboratory Animals and the guidelines of the Vanderbilt Animal Care Committee. Physiological recording techniques as well as the surgical procedures have been described[7,33].

Stimuli and apparatus. The experiments were under the control of two PC computers using software developed by Reflective Computing (St. Louis, Missouri), which presented the stimuli, recorded action potentials and eye movements sampled at 1 kHz and 250 Hz, respectively, and delivered the juice reward. Monkeys were seated in an enclosed chair within a magnetic field to monitor eye position with a scleral search coil. Stimuli were presented on a video monitor (70 Hz non-interlace, 800 × 600 resolution) viewed binocularly at a distance of 57 cm in a dark room. The background was uniform dark gray (CIE x = 205, y = 234) with a luminance of 0.07 cd/m^2. The fixation spot was a white (30 cd/m^2) square subtending 0.1°, circumscribed by a larger, 0.2° square outline of the same color and luminance, which remained on the screen at all times. The stimuli were either red (CIE x = 621, y = 345) or green (CIE x = 279, y = 615) matched for luminance (red, 2.29 cd/m^2; green, 2.30 cd/m^2) and could be either crosses or outline circles.

Behavioral procedure. Each experimental session started with a block of approximately 150 detection trials (Fig. 1a) that instructed monkeys what the target would be in conjunction search trials for that session. The target stimulus could be a combination of two colors (red or green) and two shapes (cross or circle). Each detection trial began with the presentation of a central fixation point. After an interval of fixation (400–500 ms), the target stimulus for the session was presented. Monkeys were rewarded for making a single saccade to the target within 2 s of search array presentation.

The procedure for conjunction search trials was essentially the same as for the detection trials except that the target was presented among 3 or 5 distractors. In the 4-stimulus configuration (Fig. 1b), the target was presented along with a distractor that had the target color but not the target shape ('same-color' distractor), another distractor that had the target shape but not the target color ('same-shape' distractor), and a distractor that had neither the target color nor the target shape ('opposite' distractor). In the 6-stimulus display, there was an additional same-color distractor and an additional same-shape distractor. With these choices, both displays were balanced for the number of stimuli containing any given color or shape. The stimuli, spaced evenly on the circumference of an imaginary circle around fixation, were placed such that one stimulus always fell in the center of the neuron's receptive field. On average, monkeys ran approximately 600 conjunction search trials during recordings from each neuron.

Spike density function and time of target discrimination. The spike density function was generated by convolving action potentials with a function that resembled a postsynaptic potential: $A(t) = [1 - \exp(-t/\tau_g)][\exp(-t/\tau_d)]$. Physiological data from excitatory synapses estimate the growth constant τ_g at approximately 1 ms, and the decay constant τ_d at approximately 20 ms[37].

The time at which target discrimination started was determined as follows. First, we derived the spike density function for all the correct trials in which the target fell in a neuron's receptive field and the spike density function for all the correct trials in which a distractor fell in the receptive field. The difference between these two spike density functions reflected the discrimination process. The time at which the difference function crossed a baseline difference (determined during an interval of 50 ms before stimulus presentation) was selected as the time of target discrimination only if the difference function continued to grow past the baseline difference plus 3.5 standard deviations of the baseline difference, and if it did not drop below that level for at least 50 ms.

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