

# A visual salience map in the primate frontal eye field

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**Abstract:** Models of attention and saccade target selection propose that within the brain there is a topographic map of visual salience that combines bottom-up and top-down influences to identify locations for further processing. The results of a series of experiments with monkeys performing visual search tasks have identified a population of frontal eye field (FEF) visually responsive neurons that exhibit all of the characteristics of a visual salience map. The activity of these FEF neurons is not sensitive to specific features of visual stimuli; but instead, their activity evolves over time to select the target of the search array. This selective activation reflects both the bottom-up intrinsic conspicuousness of the stimuli and the top-down knowledge and goals of the viewer. The peak response within FEF specifies the target for the overt gaze shift. However, the selective activity in FEF is not in itself a motor command because the magnitude of activation reflects the relative behavioral significance of the different stimuli in the visual scene and occurs even when no saccade is made. Identifying a visual salience map in FEF validates the theoretical concept of a salience map in many models of attention. In addition, it strengthens the emerging view that FEF is not only involved in producing overt gaze shifts, but is also important for directing covert spatial attention.

## Introduction

Although we usually look at the things that capture our attention, we are considerably limited in that we can direct our gaze toward only one narrowly focused region of the visual world at a time. To overcome this limitation, we normally inspect complex visual scenes using sequences of fast ballistic eye movements, called saccades, to direct our high acuity fovea to interesting or “attention-grabbing” locations for further visual processing. However, selective attention can also be directed to discrete locations in the visual field without saccades, which improves perception at the attended location relative to

nonattended locations (Kinchla, 1992; Egeth and Yantis, 1997). Recent research indicates that saccade target selection and visual spatial attention are implemented via a common mechanism. Behavioral studies have shown that before a saccade, visual attention is directed to the saccade target (Kowler et al., 1995; Deubel and Schneider, 1996). Neurophysiological studies, including those involving functional brain imaging, have also supported the view that covert attention and overt eye movements are functionally related (reviewed by Nobre, 2001; Corbetta and Shulman, 2002).

When viewing a scene, our attention and gaze are often directed to conspicuous objects that stand out from the background. Visual conspicuousness occurs when an object has a unique feature (e.g., color, luminance, orientation, motion, size, etc.) that sets it apart from the rest of the image. When an object is

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visually conspicuous, it captures attention through a bottom-up process. Bottom-up refers to the automatic, preattentive processing that occurs in a massively parallel manner across the entire visual field and is based exclusively on the properties of the image. In contrast, top-down refers to selection based on cognitive factors such as the goals and knowledge of the viewer. Most frequently, attention and gaze are guided by a combination of bottom-up and top-down influences (Yarbus, 1967).

Many computational models have been proposed to explain how selective attention and gaze are controlled. A common theme in many of these models is a topographic map of visual salience that specifies locations for further processing (Koch and Ullman, 1985; Treisman, 1988; Cave and Wolfe, 1990; Henderson, 1992; Olshausen et al., 1993; Wolfe, 1994; Findlay and Walker, 1999; Itti and Koch, 2001). A salience map results from the convergence of multiple feature maps, each of which encodes contrast within a single feature dimension such as color or motion. The result of this convergence is a scalar, two-dimensional map whose activity topographically represents visual salience. It has the following characteristics. First, it is not sensitive to specific features of visual stimuli such as color or motion. Second, it represents bottom-up, image-based salience; the intrinsic salience derived from the physical properties of objects regardless of what feature or combination of features is responsible for rendering salience. Third, the salience map reflects top-down influences such as the knowledge and goals of the viewer. Fourth, a winner-take-all competition within this map gives rise to a single location that corresponds to the most salient object, and specifies the target for the overt gaze shift, if one is made. Finally, the salience map is not a saccade command; it controls the allocation of attention with or without eye movements.

Does such a salience map actually exist in the brain? Recent work has pointed to brain structures within the visuomotor system that are possible candidates for containing a visual salience map. Among these are the pulvinar (Robinson and Petersen, 1992), the posterior parietal cortex (Robinson et al., 1995; Steinmetz and Constantinidis, 1995; Gottlieb et al., 1998; Kusunoki et al., 2000), the superior colliculus (Basso and Wurtz, 1998; Findlay and Walker, 1999;

McPeck and Keller, 2002), and the frontal eye field. This review will focus on recent neurophysiological evidence obtained from the frontal eye field of monkeys performing visual search tasks.

### The frontal eye field

The frontal eye field (FEF) is located in the rostral bank of the arcuate sulcus in the prefrontal cortex of macaques and is undeniably a part of the oculomotor system (Fig. 1). Low-intensity electrical stimulation in FEF elicits saccades that are topographically organized (Bruce and Goldberg, 1985), and reversible inactivation of FEF prevents saccades (Dias et al., 1995; Sommer and Tehovnik, 1997). Two types of neurons found in the FEF are directly related to gaze. Movement neurons are active before and during

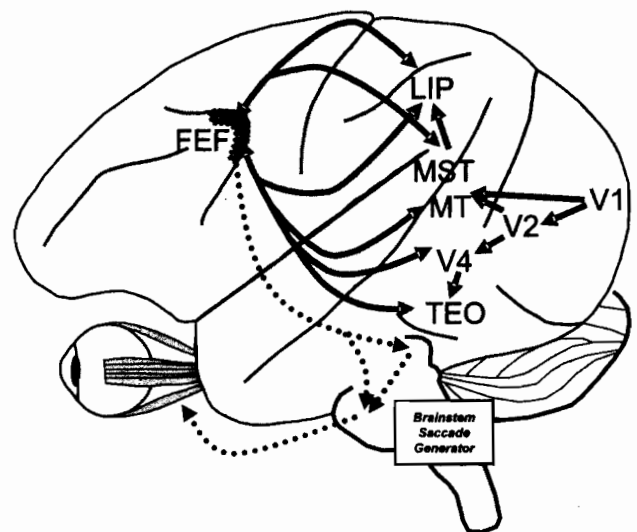


Fig. 1. Connectivity within the primate visuomotor system. Visual information from multiple visual cortical areas converges onto the frontal eye field (FEF). The central field representation of retinotopically organized areas such as V4, TEO, and MT, project to the ventrolateral portion of FEF. This part of FEF produces short amplitude saccades. The peripheral field representation of retinotopically organized areas such as LIP, as well as areas that overrepresent the peripheral visual field (e.g., MST), project to the ventrolateral portion of FEF. This part of FEF produces long amplitude saccades. The connections between FEF and visual cortex are reciprocal. The FEF sends an eye movement command to the superior colliculus and brainstem saccade generator, which send a motor signal through the cranial nerves to the eye muscles.

saccades, and fixation neurons are active while gaze is held steady (Hanes et al., 1998). Movement and fixation neurons are located in layer 5 and innervate the superior colliculus and parts of the neural circuit in the brainstem that generates saccades (Segraves and Goldberg, 1987; Segraves, 1992).

The frontal eye field is also a part of the visual system (reviewed in Schall et al., 2003). In fact, FEF is ideally positioned to contain a map of visual salience for guiding selective spatial attention and eye movements. FEF is reciprocally connected with both the dorsal and ventral visual processing streams, and these connections are topographically organized (Schall et al., 1995b). About half of the neurons in FEF have visual responses with spatially defined receptive fields (Bruce and Goldberg, 1985).

The visual cortex is organized into functionally specialized areas that contain neurons that are tuned to one or a few feature dimensions (Livingstone and Hubel, 1988; Zeki, 2001). The preattentive processing in these areas corresponds conceptually to the feature maps in the theoretical models of visual search (reviewed in Itti and Koch, 2001). FEF receives the signals from extrastriate visual cortex representing specific features such as form, color, and direction of motion. However, FEF visually responsive neurons do not exhibit selectivity for specific features (Mohler et al., 1973; Schall et al., 1995a); instead they exhibit selective activation that is related to the overall behavioral relevance of stimuli, whether relevance is derived from the intrinsic properties of the stimuli or from the viewer's knowledge and goals. In the remainder of this chapter we will summarize the evidence that demonstrates that the selective activation in FEF is compatible with the theoretical salience map. First, we will look at whether selective activation in FEF reflects visual selection or saccade preparation.

### Visual selection or saccade preparation

The visual search paradigm has been used extensively to investigate visual selection and attention (Treisman, 1988; Wolfe, 1998). In a visual search task, multiple stimuli are presented, and from among them a target is discriminated. The term "popout" refers to the search condition in which the target can

be distinguished from distractors with seemingly no effort, such as a red spot among several green spots. To investigate how the brain selects targets for visually guided saccades, recordings of neural activity were made in the FEF of monkeys trained to shift gaze to an oddball target stimulus in a popout search array (Schall et al., 1995a). Most visually responsive neurons in FEF responded initially indiscriminately to the target or the distractor of the search array in their receptive field. However, before a saccade shifted gaze to the target, a discrimination process transpired by which most visually responsive neurons in FEF ultimately signaled the location of the oddball target stimulus. Thus, instead of representing specific features of objects, visual neurons in FEF represent the behavioral relevance of objects. But is the selection observed in FEF an explicit representation of the visual search array that identifies the oddball stimulus, or does it simply reflect the generation of the saccade to that object?

To distinguish between visual selection and saccade preparation, an analysis was carried out to determine when the selection was accomplished in relation to the time of the presentation search array and the time of the saccade (Thompson et al., 1996). It was found that FEF visual neurons discriminate the target from the distractors in a pop-out search array at a fairly constant interval after search array presentation (Fig. 2A). In other words, the time at which the target of the saccade was identified did not predict when the eyes moved. This finding demonstrated that, in an easy popout search task, a relatively constant period of time is taken to identify the saccade target, and the variability in saccade reaction time is due to variability in the time needed to prepare and execute the eye movement.

Are saccades necessary for selection? The same monkeys that were trained to make a saccade to the oddball in the popout search experiment (Schall et al., 1995a; Thompson et al., 1996) were also trained in a NOGO version of the visual search task (Fig. 2B). The monkeys were rewarded for maintaining fixation while passively viewing the visual search array (Thompson et al., 1997). In NOGO search, FEF visual neurons still discriminated the oddball from distractors at the same time and to the same degree as when a gaze shift was produced in the search task in which saccades were made.

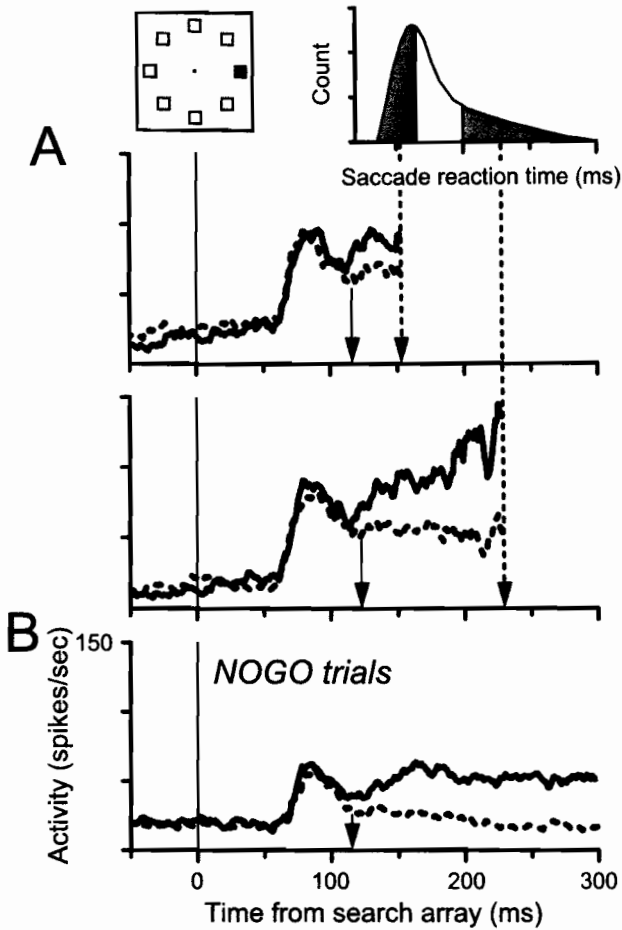


Fig. 2. Visual selection of a conspicuous target by an FEF visual neuron. Each plot shows the average activation when the oddball stimulus appeared in the neuron's receptive field (solid lines), and when distractors appeared in the receptive field (dotted lines). The initial 100 ms of activation following the presentation of search array did not discriminate the oddball from distractors. After 100 ms, the response to the oddball grew and the responses to the distractors were suppressed. (A) The top two plots show the average activity, grouped according to reaction time, during a block of trials in which the monkey made a saccade to the oddball. The ranges of reaction times selected for analysis are indicated by the shaded regions of the reaction time distribution in the upper right plot. As reaction time increases (dotted arrows), the time of target selection does not (solid arrows). (B) The activity of the same neuron during a block of trials in which the monkey was instructed to withhold a saccade while passively viewing the same search array. When no saccade was produced, the overall activation was attenuated, but the same selection process was observed. Thus, selection was not contingent on saccade production (from Thompson et al., 1996, 1997).

The question of whether the visual selection in FEF necessarily leads to a saccade to the selected location was addressed further in an experiment in which the target of a search array changes location before the monkey can make a saccade (Murthy et al., 2001). In the search-step task, most trials were identical to the popout search task in which the monkey was rewarded for making a single saccade to the oddball, but on about a third of the trials the target unexpectedly switched places with a distractor. The monkeys' task was to shift gaze to the new target location to receive a juice reward. The timing of the target step was adjusted so that the monkeys were able to compensate for the target step on about half the trials. On the remaining trials the monkeys did not compensate for the target step and made a saccade to the original target location and were not rewarded. The question to be answered was: Does the selective activation track the location of the popout target or does the selective activation predict the monkey's impending eye movement? The answer is that the selective activity reflects the location of the salient visual stimulus, not the monkey's behavior (Fig. 3). This was most evident on those trials in which the first stimulus presented in the receptive was a distractor, and then changed to the target.

Based on the evidence, we conclude that the selection signal in FEF is an explicit representation of the oddball stimulus and is independent of saccade production. However, in these experiments visual salience was not manipulated; the visual stimulus was always a search array in which the oddball stimulus was easily discriminated from the distractors. In the next section, we will show that FEF neurons reflect the intrinsic salience present in a visual scene.

### *Bottom-up salience in FEF*

A yellow flower in a field of red flowers, a flash of a light, or one person running in a crowd of people will all automatically and involuntarily capture attention. At the very least, a salience map must reflect this intrinsic conspicuousness of objects in the visual environment. Salience that is derived solely from the physical properties of the stimuli is termed *bottom-up* because it reflects the sensory stimulation coming from "lower" visual areas, and is computed in a

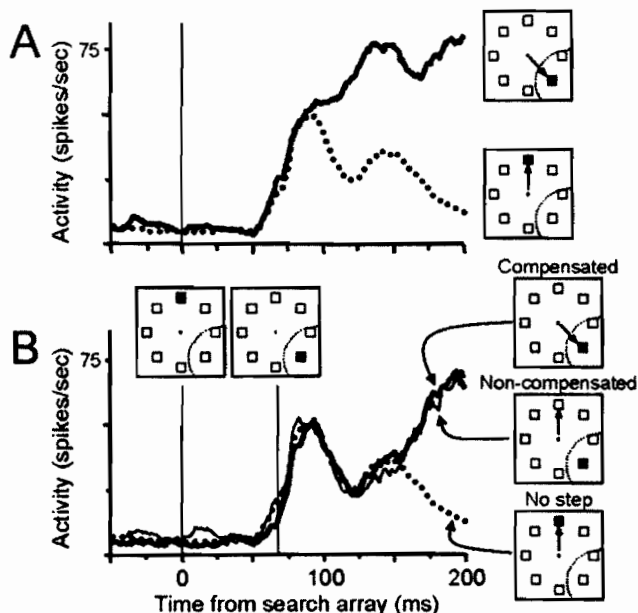


Fig. 3. The dissociation of visual selection in FEF and saccade production is revealed with the search-step task. In the search-step experiment, most of the trials were identical to the popout search task shown in Fig. 2. But on about 1/3 of the trials the oddball target and a distractor switched places before the monkey could make a saccade to it. The monkey was rewarded for making a saccade to the new target location. (A) The activation on no-step trials when the target (solid line) or distractors (dotted line) fell in the receptive field (indicated by dotted area in the stimulus arrays). (B) The activation on step-trials when the distractor in the receptive field unexpectedly became the target. On compensated trials (thick solid line), the monkey successfully shifted gaze to the new target location. On noncompensated trials (thin solid line), the monkey shifted gaze to the original target location outside the neuron's receptive field. Initially, the activity on step trials (solid lines) was identical to that on the distractor-evoked activity on no-step trials (dotted line). After about 130 ms following the target appearing in the receptive field, the activity on both compensated (thick line) and noncompensated (thin line) trials grew equally strong. The selective activity of this neuron corresponded to the shifting location of the oddball stimulus, not to the monkey's saccade (from Murthy et al., 2001).

preattentive manner across the entire visual field. Of course, not every object carries the same degree of intrinsic visual salience, and the theoretical salience map should reflect these differences.

The contribution of intrinsic visual salience to the selection process in FEF was investigated in two experiments. In one, the similarity of the oddball target and distractors was manipulated (Bichot et al., 2001b; Sato et al., 2001). In the other experiment,

the monkey searched for the oddball shape in a search array in which one of the distractors was a different color (Bichot et al., 2001a).

#### *Effect of target-distractor similarity*

The monkey's task of finding the target among the many distractors was made easy or hard by making the target very different or more similar to the distractors. Both color and motion search were investigated. In color search, target discriminability was reduced by using similar colors for the target and distractors. In motion search, each stimulus was a circular aperture of randomly positioned dots, a proportion of the dots translated coherently in a specified direction and the rest of the dots were replotted randomly. The direction of motion was either left or right, and the motion of the target was opposite from that of the distractors. Target discriminability was manipulated by changing the proportion of dots that moved coherently. To change the target's discriminability in both color and motion search, either the target or the distractors could change randomly from trial to trial. However, whether it was the target or the distractors that changed remained consistent within a recording session. The monkeys' performance showed that the manipulation was effective; on hard search trials, the monkeys made more errors and had longer reaction times than on easy search trials. Regardless of how target-distractor similarity was manipulated, the results were essentially the same (Sato et al., 2001).

On the theoretical salience map, the salience of any object is dependent on the relative levels of the activity peaks across the map. In this experiment, the salience level would be measured as the difference between the target and distractor representations. Figure 4 shows the pooled activity of 39 visually responsive neurons recorded during the color easy/hard search task in which the distractors were always green and the target alternated randomly between either red (easy trials) or yellow-green (hard trials). On correct trials (Fig. 4A), the target selection process in FEF identified the oddball stimulus, but the magnitude of selection reflected search difficulty and therefore, is consistent with the salience map model. Before the saccade to the oddball target, the

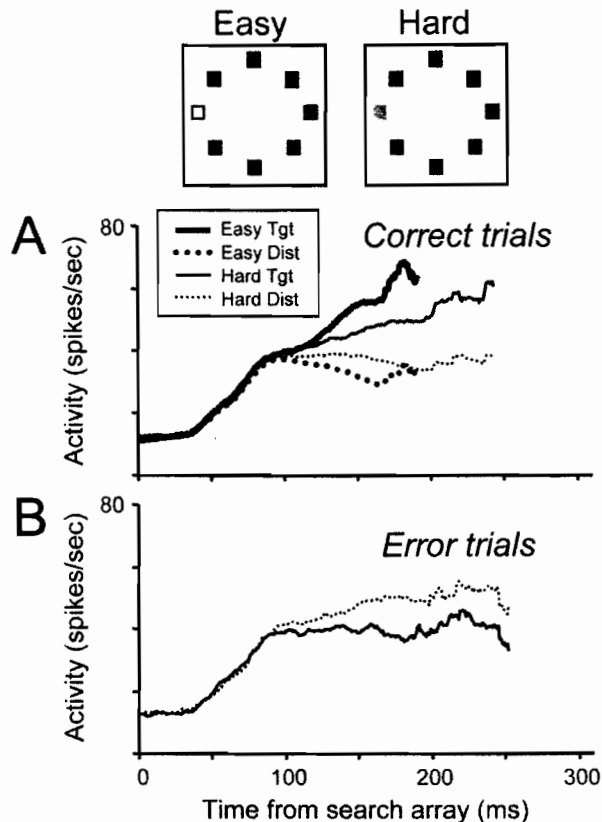


Fig. 4. Effect of target-distractor similarity on visual selection. Easy search trials were interleaved with hard search trials and the monkeys' task was to shift gaze to the oddball stimulus. Target-distractor similarity was manipulated by changing the color of the target; the color of the distractors was the same on every trial. (A) The pooled response of a population of visual neurons recorded during the easy-hard search task. Neural activity is plotted until the average time of saccade initiation for each trial type. The difference in response to the target (solid lines) and distractors (dotted lines) (i.e., the magnitude of selection) was greater on easy trials (thick lines) than on hard trials (thin lines). (B) The pooled response of the same neurons on hard search trials when the monkeys incorrectly made a saccade to a distractor. There was greater activation for the distractor the monkey looked at (dotted line) than for the oddball target (solid line) (from Thompson et al., 2004).

difference between the target and distractor evoked activity reached a greater value on easy trials than on hard trials. The reduced magnitude of selection in hard trials as compared to easy trials was a result of both a decrease in the target response and an increase in the distractor response. It is noteworthy that for the data shown in Fig. 4 the distractor stimuli were physically identical on both easy and hard trials. Therefore, the greater activity in response to the

green distractor on hard trials reflects its greater similarity to the oddball target.

The peak on the theoretical salience map specifies the target for the saccade. When the distractor representation on the salience map approaches that of the target, there is a greater probability that on any one trial the activation to a distractor will exceed that of the target and an incorrect saccade will be made to the distractor. Consistent with this prediction, Bichot et al. (2001b) showed that the differences in the magnitude of selection between easy and hard search is correlated with the monkey's probability of making a correct saccade to the oddball stimulus across different search conditions. Recently, we analyzed the activity of FEF neurons recorded on error trials during visual search (Fig. 4B) (Thompson et al., 2004). There were enough error trials to analyze for the hard search condition, but not for the easy search condition. On trials in which the monkey made a saccade to one of the distractor stimuli, the activity in FEF representing that distractor was slightly greater than the activity representing the oddball target stimulus. Therefore, the highest peak of activity in FEF corresponds to the endpoint of the forthcoming saccade, even when that saccade was not to the most physically salient stimulus. However, the magnitude of selection on error trials was less than on correct trials even though the saccades were identical. This pattern is more consistent with the hypothesis that FEF selective activity represents visual salience than with the alternate hypothesis that the selective activity in FEF is directly related to saccade production.

#### *Effect of a salient distractor*

In some instances, the item sought by a viewer in one feature dimension may not be the most salient item in the image. The presence of such singleton distractors has been shown to disrupt performance (Theeuwes, 1991). If the target selection signals in FEF represent the saccade goal only, the representation of such a singleton distractor should not differ from that of other distractors on trials in which the viewer correctly locates the less-salient oddball target. On the other hand, if activity in FEF represents forms a visual salience map, the intrinsic salience of

the singleton distractor should manifest itself in that map.

Monkeys performing a search task for a shape singleton exhibited slower reaction times and increased error rates when the search array included a color singleton distractor to be ignored (Bichot et al., 2001a) (Fig. 5). During correctly performed popout search trials with a singleton distractor, neural modulation in FEF reflected the behavioral significance of all stimulus types. After an initial period of nonselective visual responses, neurons exhibited the highest activation for the popout shape target in their response field. But interestingly,

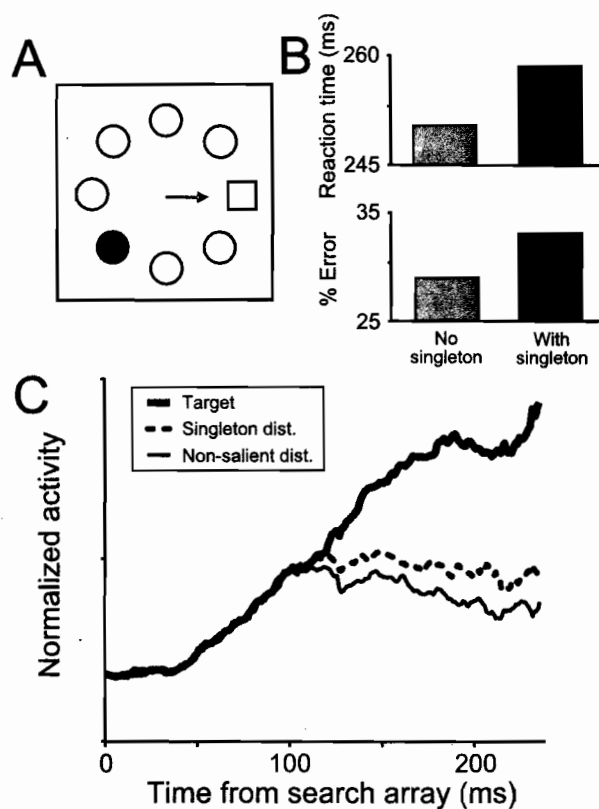


Fig. 5. Effect of a conspicuous color singleton distractor during a shape popout search. (A) Task display. (B) Mean saccadic reaction time and error rate during the shape search task with (black bars) and without the color singleton (gray bars). The proportion of saccades to the color singleton is represented by the white stripes. (C) Pooled normalized response of a population of FEF visually responsive neurons during correctly performed feature search trials with a singleton distractor. Responses to the target (thick solid line), to the singleton distractor (dotted line), and to the nonsalient distractors (thin solid line) are shown superimposed (from Bichot et al., 2001a).

they responded to the singleton distractor significantly more strongly than to nonsalient distractors in their response field. Thus, FEF neurons signal intrinsic visual salience of objects even when they are not the goal of the search task.

### Top-down salience in FEF

In order to effectively guide attention and goal directed behavior, a salience map must incorporate the subject's expectations, knowledge, and the learned values associated with different objects in the visual world. For example, a mother can easily find her own child among a group of children; and this ability is greatly enhanced if she knows the color of the clothes the child is wearing. The mother's memory of her own child's distinctive characteristics and the knowledge of the child's clothing both improve her ability to locate her child. These are two examples of visual salience resulting from *top-down*, or cognitive, processes. The importance of cognitive, or top-down, factors in the FEF selection process has been demonstrated in a number of experiments.

### Knowledge of feature dimension

We are better at detecting an object in a visual scene when we know something about its features, such as its color or shape (reviewed in Corbetta and Shulman, 2002). In this case, we are able to limit our search to one feature dimension. One example of this top-down control is found in the visual search experiment with a singleton distractor described in the previous section (Fig 5). In that experiment, the monkey learned to perform a visual search task for an oddball shape, but the odd-shaped target was not the most conspicuous object in the search array. The most conspicuous object was the color singleton, and it did elicit the highest activation among the distractors. However, the highest activation was for the odd-shaped target stimulus. Therefore in this task, FEF activity reflects the learned top-down goal of the search to find the odd shape, as well as the bottom-up intrinsic salience of the irrelevant singleton distractor.

### Effect of memory

In many real-world situations, an object of interest cannot be located based on conspicuity, and a memory of that object is required to locate it (e.g., “searching for a face in the crowd”). An analogous situation is obtained during a conjunction search where the target is defined by one combination of possible features, and distractors are formed by other possible combinations. Many studies have shown a dichotomy between feature (or popout) search that appears to be effortless since performance is not affected by the number of distractors in the display, and conjunction search that appears more attentionally demanding since performance worsens to some degree with increasing number of distractors. This dichotomy has played an important role in the development of theories of visual attention, including the guided search model postulating that stimuli during conjunction search can be processed in parallel to identify those with the desired features (Wolfe, 1994).

To the extent that attention and eye movements are functionally related, such a parallel search strategy predicts that subjects would be more likely to shift gaze to a distractor that shares a target feature (i.e., “similar distractor”) than to a distractor that has no features in common with the target (i.e., “opposite distractor”). We have confirmed this prediction in monkeys searching for a target defined by the combination of color and shape (Bichot and Schall, 1999) (Fig. 6). Interestingly, when target properties remained the same within an experimental session, but changed across experimental sessions, we also found evidence that the history of target properties affected behavior revealed by an increased tendency of errant saccades to land on the distractor that was the search target during the previous session.

Recordings in FEF during conjunction search further support the hypothesis that this area represents a visual salience map derived from bottom-up and top-down influences. After the initially nonselective response, FEF neurons not only discriminated the target from distractors, but also discriminated among the distractors based on their visual similarity to the target and the history of target properties across sessions (Fig. 6). In other words, while the highest activation was associated with the target, the responses to distractors similar

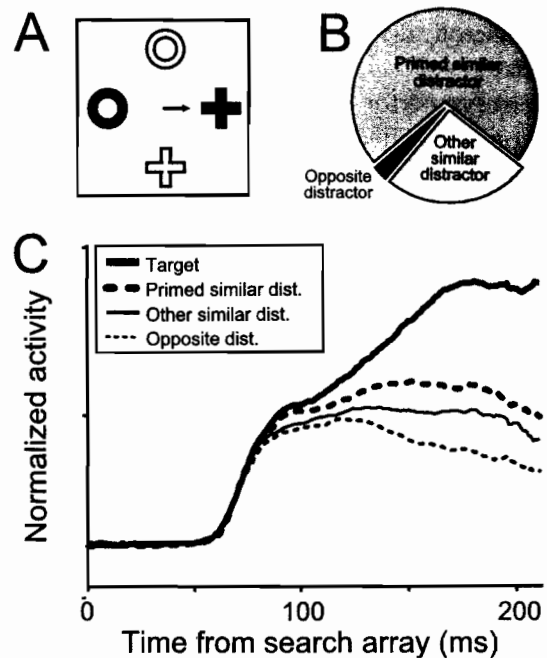


Fig. 6. Visual selection of a remembered target during conjunction search. (A) Conjunction search display. The arrow indicates the saccade to the correct target. (B) Probability of shifting gaze to each distractor type. On error trials, saccades were most often directed to a similar distractor that shared one of the features of the target. Errant saccades exhibited an additional tendency to be directed to the distractor that had been the target in the previous experimental session (primed distractor). (C) Normalized pooled response of a FEF visually responsive neurons during correctly performed conjunction search trials (i.e., first and only saccade was made to the target). The highest response was to the target (thick solid line), followed by the primed similar distractor (thick dotted line), then unprimed similar distractor (thin solid line), and the lowest response was to the opposite distractor (thin dotted line) (from Bichot and Schall, 1999).

to the target and to distractors primed by virtue of being the target of the previous session were relatively enhanced. Thus, this study shows that neural modulation in FEF reflects a variety of top-down influences, and predicts covert and overt orienting patterns during a complex visual search. Furthermore, since the above similarity- and priming-based modulations were observed during correctly performed trials in which a single saccade was made to the target, these results rule out the possibility that the selection signal in FEF represents nothing more than a command to move the eyes.

Further evidence that a template of the target held in memory can influence the target selection process



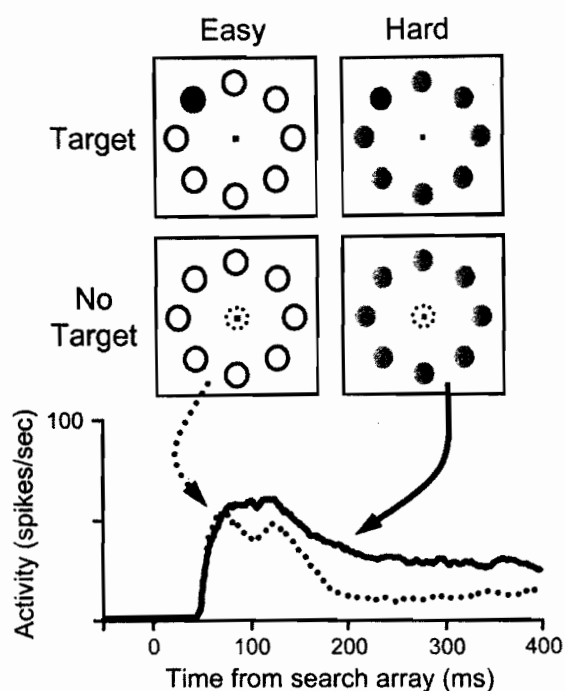


Fig. 7. Effect of memory when no target is present. On each trial, after the monkey fixated the central spot one of the displays at the top were presented at random. On target trials the monkey was rewarded for shifting gaze to the oddball. The target feature was the same on every trial so the monkeys could remember what the target looked like from trial-to-trial. Target-distractor similarity was manipulated by changing the distractor feature. On no-target trials the visual display could be made up of either the distractors that were different from the target (easy) or the distractors that were similar to the target (hard), and the monkeys were rewarded for maintaining fixation on the central fixation spot. The plot compares the pooled population responses on easy and hard no-target trials. Although no eye movements were made, the response to the distractors that were similar to the remembered target (hard no target trials) was greater than the response to the distractors that were different from the remembered target (easy no target trials) (from Sato et al., 2003).

in FEF was obtained from the easy-hard search experiment discussed in the previous section (Sato et al., 2003). In many recording sessions the target remained constant from trial to trial and the salience of the target was manipulated by changing the distractor feature. During those sessions, on a fraction of trials the target was absent and only distractors were presented and monkeys were rewarded for maintaining fixation on the central spot. Even in trials with no target present, the activation of FEF neurons in response to distractors was proportional to the visual similarity of the

distractors to the remembered target (Fig. 7). Because no eye movements were made, and a target was not available for a direct comparison with the distractor features, this modulation can be solely attributed to the top-down influence of memory.

#### *Perceptual priming*

The performance of both humans and monkeys during popout search is affected by experience (McPeck et al., 1999; Bichot and Schall, 2002). This robust effect, known as perceptual priming, manifests itself as an improvement of behavioral performance with the repetition of stimulus features over consecutive trials (Fig. 8).

We found that the properties of the neural selection signals in FEF could fully explain changes in behavior due to priming (Bichot and Schall, 2002). Neurons discriminated the target from distractors earlier and better with repetition of stimulus features, corresponding to improvements in saccade latency and accuracy, respectively (Fig. 8). Furthermore, consistent with earlier psychophysical explorations of priming of popout, the improvement in the neural target selection signals consisted of both target enhancement and distractor suppression. Moreover, the timecourse of neural discrimination in FEF accounted for the increase in saccade latencies associated with the location-based inhibition of return when target position repeated across consecutive trials. These results showed that the neural selection process in the FEF mirrored the dynamic changes in performance due to the monkeys' experiencing sequential regularities in display properties across trials.

#### *Effect of a prolonged cognitive strategy*

An extreme example of a perceptual bias developed after extensive training on only one complement of a search array (e.g., always a red target among green distractors) (Bichot et al., 1996). We found that monkeys' search strategy and the concomitant neural selection process in FEF can be modified profoundly by a prolonged cognitive strategy. When monkeys were given exclusive experience with only one visual search array, they adopted a strategy of ignoring

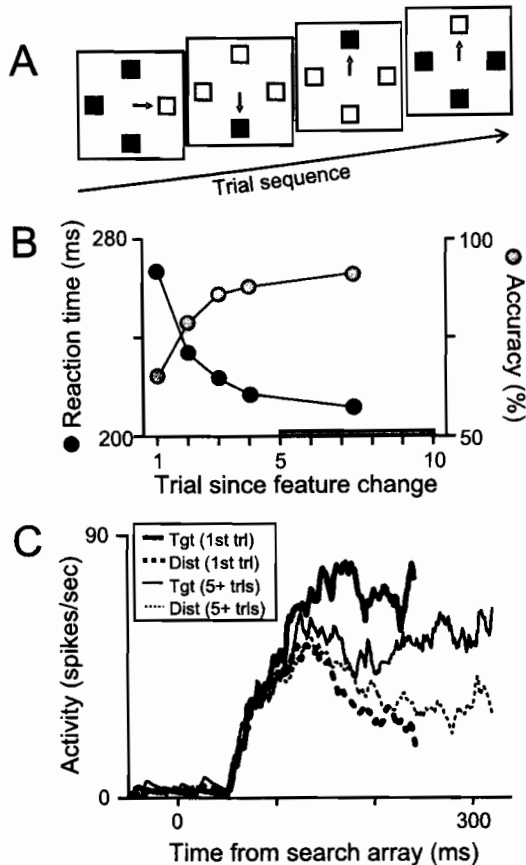


Fig. 8. Effect of feature expectation during a color popout search. (A) Task display sequence for four trials. The arrow illustrates the saccade to the target. In this sequence, the second trial represents the first trial after a feature switch, the next trial represents the second trial after the feature switch; and the last trial represents another first trial after a feature switch. (B) Mean saccade latency and accuracy as a function of trial number since feature switch. (C) Response of one FEF visuomotor neuron to the target (thick solid line) and to distractors (thick dotted) during trials immediately following a feature switch, and to the target (thin solid) and distractors (thin dotted) during trials more than four removed from the feature switch. Neural activity is plotted until the average time of saccade initiation for each trial condition. The difference in response to the target and distractors (i.e., the magnitude of selection) was greater on trials far removed from the feature switch than on the first trial after the feature switch (from Bichot and Schall, 2002).

stimuli with the learned distractor feature, even if those same stimuli became the popout stimulus in the complementary visual search array presented occasionally (Fig. 9A). In monkeys using this strategy, about half of FEF neurons exhibited a suppressed response to the learned distractor as soon as they responded (Fig. 9B). In other words, unlike

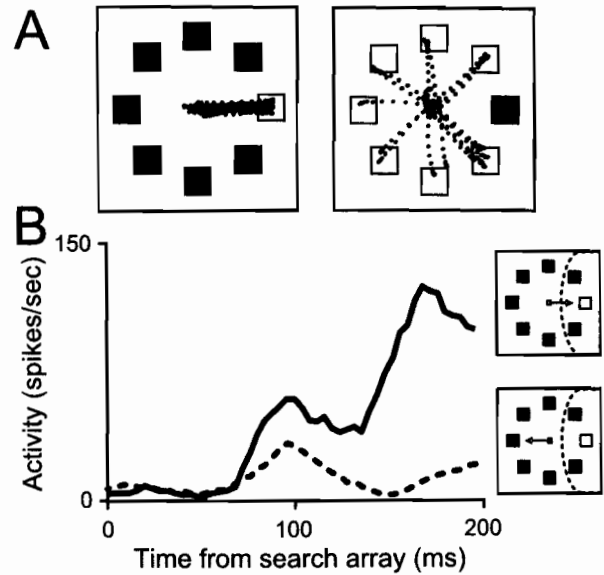


Fig. 9. Effect of a prolonged cognitive strategy on visual selection in FEF. (A) The saccade behavior of a monkey trained on just one visual search array. When presented an array in which the target and distractor colors were switched, instead of looking at the conspicuous oddball (left panel), this monkey looked at a distractor that was the same color as the target in the complementary array (right panel). (B) Response of one FEF neuron while this monkey performed search with the learned search array. Unlike what was observed in monkeys trained on both complements of the search array, in these particularly trained monkeys half of the neurons in FEF exhibited a selective response from the earliest spikes that could be measured (from Bichot et al., 1996).

what had been observed before in this area, FEF neurons exhibited apparent color selectivity in their earliest measurable response. Because the onset time of this color selectivity rivals that of primary visual cortex, we concluded that some sort of experience-dependent plasticity facilitated the processing of the learned target color. Thus, it appears that a prolonged cognitive strategy can influence preattentive, or bottom-up, processing. This study shows how cognitive strategies can dramatically affect the behavioral relevance of stimuli and their underlying neural representation in FEF even during a simple popout visual search.

## Conclusion

We have summarized the accumulated evidence from a variety of visual search experiments showing that a visual salience map exists in the primate frontal eye

field. A population of visually responsive neurons in FEF exhibits all of the characteristics of a salience map proposed by many models of overt and covert attention. First, the initial visual responses of FEF neurons are not selective for specific features such as color, shape, or direction of motion (Figs 2–8). Second, the later selective activation reflects the intrinsic, bottom-up, salience of the objects in the visual scene (Figs. 4A, 5). Third, the selective activation also incorporates top-down factors such as goals, memory, and knowledge (Figs. 6–8). Fourth, the peak of activity in FEF specifies the target for the saccade, even if it is not the most conspicuous object in the visual scene (Figs. 4B, 5). And finally, the visual selection signal in FEF is independent of saccade production (Figs. 2B and 3). Instead, the selective activation in FEF reflects the behavioral relevance of objects in the visual scene.

Identifying a salience map in FEF is important because it means that the concept of a salience map is a physiologically sound theoretical construct that can be useful in guiding future theoretical and empirical investigations of attention. It should be noted that, although we have focused on FEF, the representation of visual salience is likely distributed in a network involving many visuomotor structures such as the superior colliculus (Findlay and Walker, 1999; McPeck and Keller, 2002) and posterior parietal cortex (Gottlieb et al., 1998; Kusunoki et al., 2000).

Finally, it seems clear that the function of FEF is much more than just producing eye movements. FEF should also be considered as a part of the visual pathway for the selection of stimuli, whether covertly or overtly. This view is consistent with functional imaging studies that have shown that the human homologue of FEF is activated during both overt and covert shifts of attention (Nobre, 2001; Corbetta and Shulman, 2002). We should also consider that FEF provides feedback connections to extrastriate visual cortex (Schall et al., 1995b), and therefore selection signals in FEF can in turn modulate activity in these areas. Interestingly, a set of experiments by Moore and colleagues showed that electrical stimulation of FEF in monkeys improves perceptual ability (Moore and Fallah, 2001) and modulates visual activity in extrastriate visual cortex (Moore and Armstrong, 2003). These findings, combined with the evidence reviewed in this chapter, lead to the conclusion that

the selective activation of FEF visual neurons corresponds to the allocation of visual spatial attention.

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