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The neural selection and control of saccades by the frontal eye field

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Recent research has provided new insights into the neural processes that select the target for and control the production of a shift of gaze. Being a key node in the network that subserves visual processing and saccade production, the frontal eye field (FEF) has been an effective area in which to monitor these processes. Certain neurons in the FEF signal the location of conspicuous or meaningful stimuli that may be the targets for saccades. Other neurons control whether and when the gaze shifts. The existence of distinct neural processes for visual selection and saccade production is necessary to explain the flexibility of visually guided behaviour.

Keywords: visual attention; visual search; countermanding; reaction time

1. INTRODUCTION

Figure 1*a* shows the eye movements produced by a monkey inspecting an array of stimuli to locate a specific target. The rapid shifts of gaze that redirect the fovea of the retina, which provides high-acuity vision, onto a new point in the image are called saccades. Saccades tend to direct gaze to conspicuous features in the scene. Or, if a particular strategy or goal is employed, the gaze can then concentrate on appropriate inconspicuous elements in the image (e.g. Yarbus 1967). Natural vision is accomplished through a cycle of fixation and visual analysis interrupted by saccadic eye movements. Figure 1*b* illustrates the variability of fixation durations over time. In this short period of just nine saccades between the stimuli, the fixation durations ranged from 85 to 320 ms. Similar fixation durations have been observed in humans performing a scanning visual-search task (e.g. Hooge & Erkelens 1996), with even more variability when viewing more engaging natural scenes (Viviani 1990). These delays must arise from the processes that are carried out upon the fixation of each element and before the saccade to the next. While fixating a point in an image, at least two processes take place. First, perceptual processing analyses the object in the fovea to ascertain its identity and the image in the periphery to locate the target for the next saccade. Second, response preparation precedes the saccade. These processes take some time.

A network of structures in the brain produces and conveys the signals necessary to select a target and produce a saccade. This review focuses on the role of the FEF in the selection of targets for saccades and the control of the initiation of saccades. The kinds of neural activity and modulation observed in the FEF occur in related structures such as the superior colliculus or posterior parietal cortex. Thus, an essential fact is that the processes that will be described occur concurrently in a network of interconnected structures. This fact precludes the assignment of any particular function exclusively to a given part of the brain.

2. FRONTAL EYE FIELDS

The FEF, located in prefrontal cortex, is an area that contributes to transforming visual signals into saccade commands (reviewed by Schall 1997; Schall & Thompson 1999). Thus, the FEF has two facets—one motor and the other sensory.

The evidence for the motor function of the FEF is not controversial. Low-intensity electrical stimulation of the FEF elicits saccades (e.g. Bruce *et al.* 1985). This direct influence is mediated by neurons in the FEF that modulate activity specifically before and during saccades (Bruce & Goldberg 1985; Schall 1991; Hanes & Schall 1996; Hanes *et al.* 1995, 1998). The neurons in the FEF that generate movement-related or fixation-related activity are located in layer 5 and innervate the superior colliculus (Segraves & Goldberg 1987; Sommer & Wurtz 1998*a*, 2001) and parts of the neural circuit in the brainstem that generates saccades (Segraves 1992). These neurons, in concert with counterparts in the superior colliculus (Sparks 1978; Munoz & Wurtz 1993, 1995; Dorris *et al.* 1997; Dorris & Munoz 1998), produce signals necessary to produce saccadic eye movements. Experiments probing the control of saccades in monkeys provide evidence for the sufficiency of the activity of presaccadic movement-related neurons in the FEF to specify whether and when saccades will be produced (Hanes & Schall 1996; Hanes *et al.* 1998). Reversible inactivation studies provide evidence for the necessity of the FEF to produce saccades (Dias *et al.* 1995; Sommer & Tehovnik 1997). These findings complement earlier observations that the ablation of

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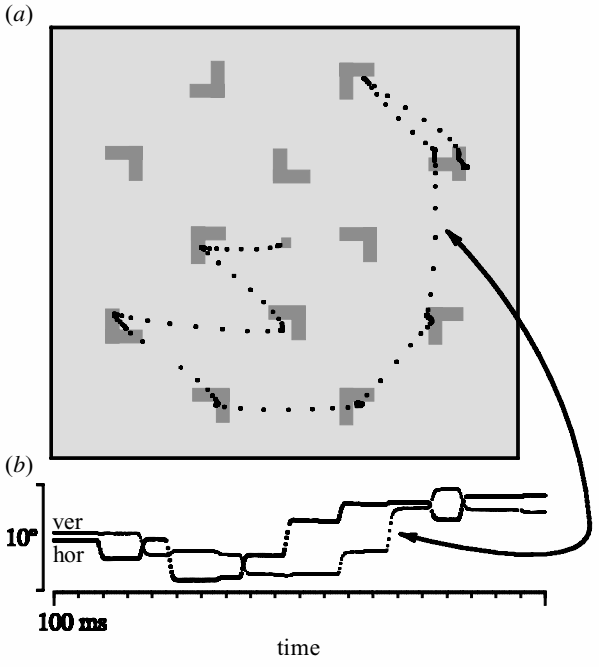

Figure 1. (*a*) Pattern of gaze shifts made by a monkey searching for a randomly orientated T shape among L shapes. The T shape among the L-shape array appeared after the monkey fixated the central square. On this trial, the monkey's first saccade was to the left, followed by a sequence of eye movements around the perimeter of the array. This leads to the question of what neural events selected certain elements but not others in the array? (*b*) Plots of eye position in the horizontal (thick) and vertical (thin) axis as a function of time during the viewing period. The first leftward saccade corresponds to the first downward deflection in the plot of eye position in the horizontal axis. The vertical saccade to the target is highlighted by the arrow. The interval spent fixating each L shape varied from less than 100 ms to *ca.* 300 ms. This leads to the question of what neural processes account for the variable amount of time spent foreating the various effectively identical elements? (Adapted from Schall & Thompson 1999.)

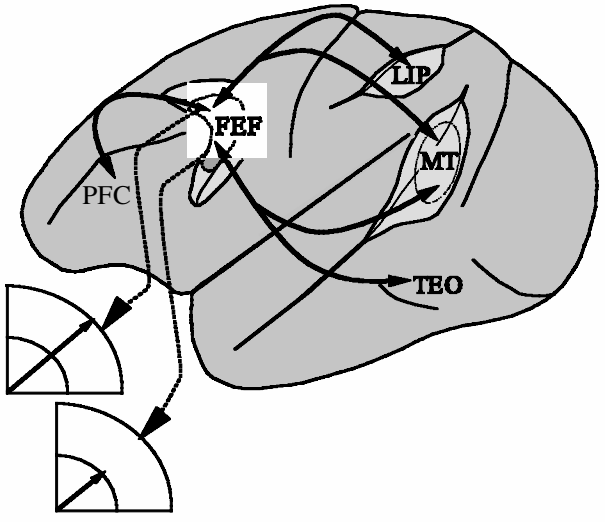

Figure 2. A summary of the connections of the FEF. The FEF contributes to the preparation and initiation of saccades through projections to the superior colliculus and brainstem saccade generator. There is a rough topographic map of saccade amplitude in the FEF; the shorter saccades are represented ventrally and the longer saccades medially. The FEF is reciprocally connected with a multitude of extrastriate visual areas in both the dorsal and ventral streams. The projections are topographically organized; the foveal representation of retinotopic areas projects to the ventrolateral part of the FEF and the peripheral representation projects to the dorsomedial part of the FEF. These diverse visual inputs convey an elaborate representation of the image to the centres that will specify which saccade to produce. The FEF is also connected with areas in the prefrontal cortex. These connections convey the influence of context that can supplement or override the outcome of visual processing. PFC, prefrontal cortex; FEF, frontal eye field; LIP, lateral interparietal area; MT, middle temporal visual area; TEO, tempero-occipital visual area.

the FEF causes an initially severe impairment in saccade production that recovers in some but not all respects over time (e.g. Schiller *et al.* 1987; Schiller & Chou 1998, 2000*a*,*b*).

The evidence that the FEF is involved in visual function is equally compelling. The FEF is reciprocally connected with a multitude of visual cortical areas in both the dorsal and ventral streams (Huerta *et al.* 1987; Baizer *et al.* 1991; Schall *et al.* 1995*b*; Stanton *et al.* 1995; Barone *et al.* 2000) (figure 2). The more ventrolateral portion of the FEF, which is responsible for generating shorter saccades, is interconnected with the perifoveal representation in retinotopically organized areas, from areas that represent central vision in the inferotemporal cortex and from other areas having no retinotopic order. The more ventrolateral portion of the FEF (which produces shorter saccades) is interconnected with the perifoveal representation in retinotopically organized areas, with areas that represent central vision in inferotemporal cortex and with other areas having no retinotopic order. By contrast, the mediodorsal FEF (which produces longer saccades) is interconnected with the peripheral visual field representation of retinotopically organized areas, with areas that emphasize peripheral vision or have no retinotopic order and are multimodal. In fact, the FEF is unique in the extent of its connectivity with the extrastriate visual cortex (Jouve *et al.* 1998). Another source of visual signals to the FEF is the central thalamus; the FEF is innervated mainly by the lateral segment of the mediodorsal nucleus as well as part of neighbouring thalamic nuclei (Huerta *et al.* 1986). Neurons in these nuclei convey visual signals to the FEF (Schlag & Schlag-Rey 1984; Sommer & Wurtz 1998*b*). Due to the extensive convergence of afferents from the thalamus and multiple extrastriate visual areas, individual neurons in the FEF receive signals representing the colour, form, depth, direction of motion and so on of objects in the image. Such convergence seems desirable for a system to select targets for gaze shifts regardless of the visual properties of the target, akin to a salience map.

While the FEF is commonly regarded as being situated rather high in the hierarchy of visual areas (e.g. Felleman & Van Essen 1991), it should not be overlooked that the FEF provides abundant connections to many extrastriate visual areas. In fact, according to a recent analysis of intracortical connectivity, the FEF may be in a feedforward anatomical relation to prestriate areas such as V4 (Barone *et al.* 2000). Thus, the FEF can influence the activation of neurons in the extrastriate visual cortex. Certainly, the visual response latencies of FEF neurons are

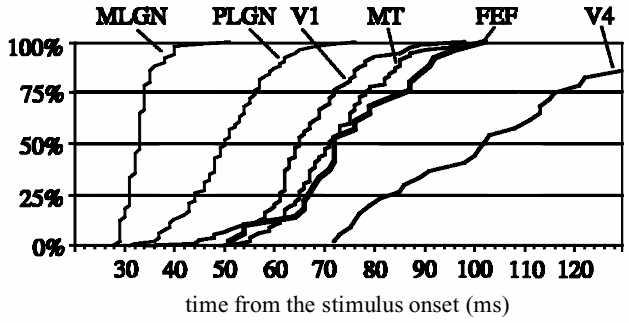

Figure 3. Cumulative distributions of the times of first response to an optimal visual stimulus are plotted for the indicated stages of the visual pathway. (Modified from Schmolesky *et al.* 1998.) MLGN, magnocellular layers of the dorsal lateral geniculate nucleus; PLGN, parvocellular layers of the dorsal lateral geniculate nucleus; V1, primary visual cortex; MT, middle temporal visual area; V4, visual area 4.

early enough to allow this possibility (Schmolesky *et al.* 1998; figure 3).

Finally, in addition to the connections with the visual cortex, the FEF is also connected to specific areas in the prefrontal cortex (e.g. Stanton *et al.* 1993). These prefrontal connections can endow the FEF with sensitivity to the context of history and goals. In other words, as described in § 3, neural responses in the FEF to a given stimulus configuration can be modulated subtly or dramatically according to the preceding experience of the monkeys.

3. SELECTION OF A TARGET AMONG UNIFORM DISTRACTORS

The visual-search paradigm has been used extensively to investigate visual selection and attention (reviewed by Egeth & Yantis 1997; Wolfe 1998). The results of many experiments distinguish two modes of visual search. One mode is the efficient visual search for, say, a black spot among several grey spots (figure 4). The second mode is the less efficient, more effortful search for, say, a randomly orientated T shape among randomly orientated L shapes (figure 1).

To investigate how the brain selects targets for visually guided saccades, we have recorded the activity of neurons in the FEF of monkeys trained to shift their gaze to the oddball target in two complementary pop-out visual search arrays (Schall & Hanes 1993; Schall *et al.* 1995*a*; Thompson *et al.* 1996; Bichot *et al.* 2001*b*). Most visually responsive cells in the FEF responded initially indiscriminately to the target or the distractor of the search array in their receptive field (figure 4*a*). The absence of a feature-selective response in the FEF during visual search is consistent with earlier work (Mohler *et al.* 1973). However, before the gaze shifted, a selection process transpired by which most visually responsive cells in the FEF ultimately signalled the location of the oddball target stimulus. Notably, in spite of the well-known variability of spiking of cortical neurons, the representation of the location of the target by FEF neurons is very reliable; combining the signals from no more than 10 selective FEF neurons is sufficient to signal the location of the target with as much fidelity as the monkeys' performance (Bichot *et al.* 2001*b*).

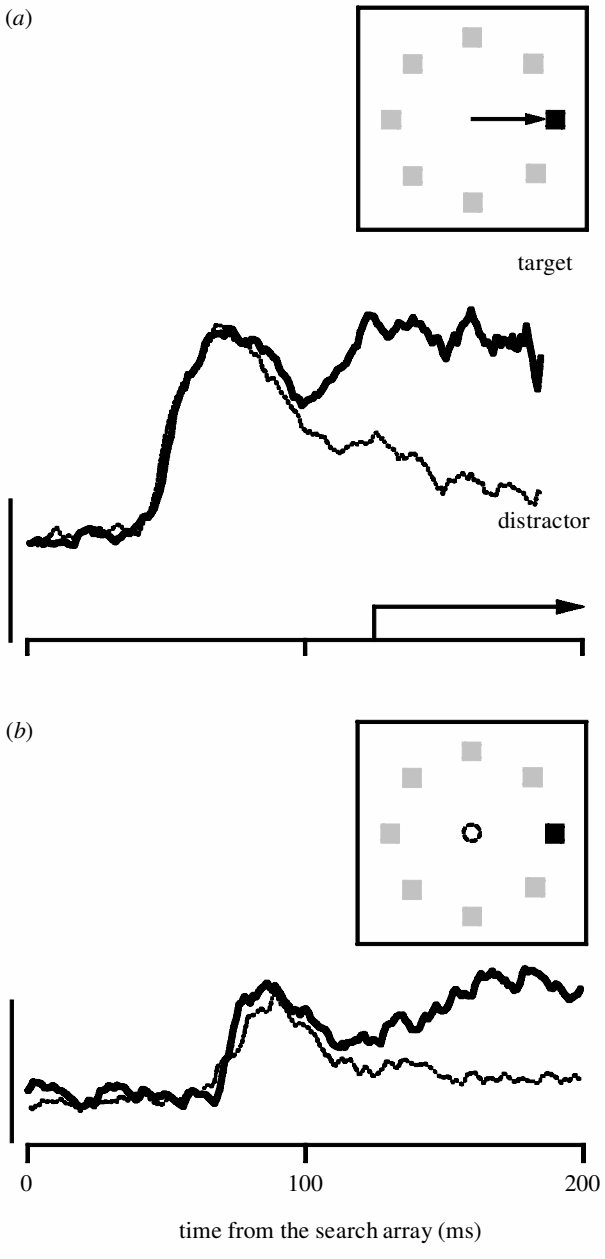

Figure 4. The activity of a FEF visual neuron after the presentation of a pop-out search array when the monkey (*a*) produced or (*b*) withheld a saccade to the oddball. Each plot shows the activation when the oddball stimulus appeared in the receptive field (solid line) and when distractors appeared in the receptive field (dotted line). When a saccade was produced to foveate the target, the initial response to the search array did not discriminate the target from a distractor. However, after *ca.* 100 ms, the activation evolved so that the neural representation of the distractors was suppressed and the activation representing the location of the target was sustained or elevated. When no saccade was produced, the level of activation was attenuated, but the same selection process was observed. Thus, the neural-selection process was not contingent on production of the saccade. The vertical scale represents 100 spikes s^{-1}. (Modified from Thompson *et al.* 1996, 1997.)

A visual target selection process has been observed in the FEF during natural scanning eye movements (Burman & Segraves 1994). Similar results have also been obtained under somewhat different conditions in the

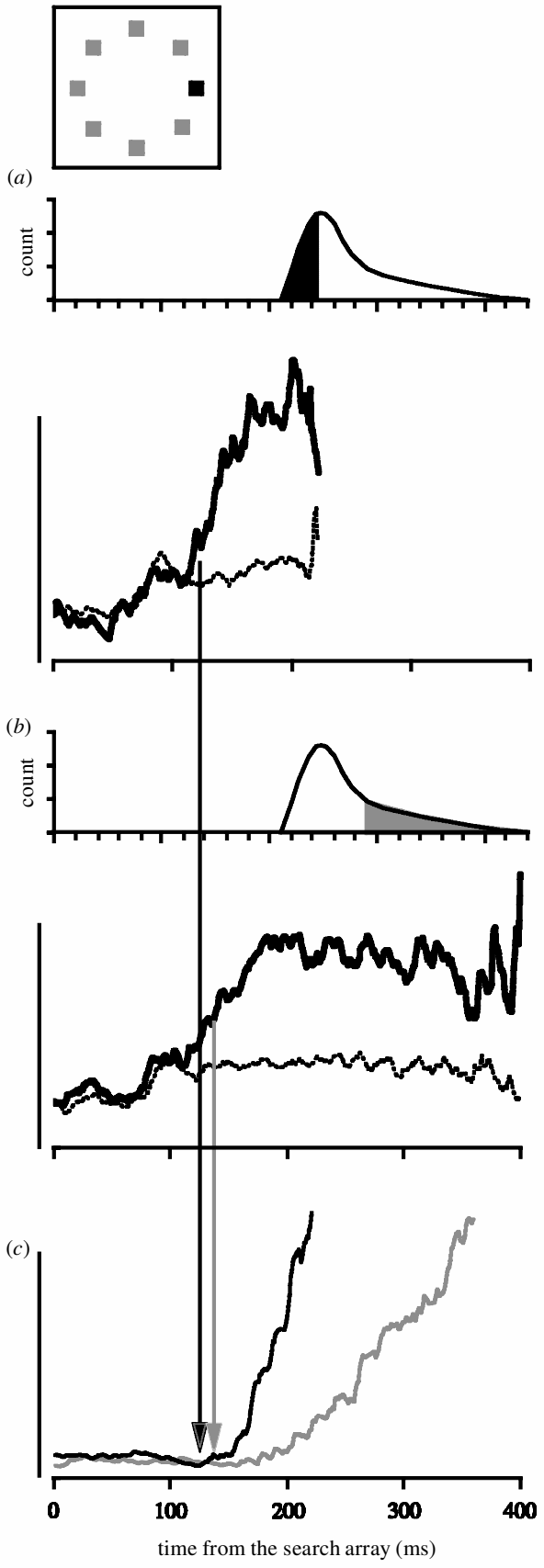

Figure 5. Relation of the time of the neural target selection to the time of the saccade initiation. The activity of a FEF neuron representing the target (thick) or distractors (thin) is shown during trials with saccades of the shortest (*a*) or longest (*b*) latencies. The upper plot in (*a*) and (*b*) indicates the distribution of saccade latencies within the range selected for the analysis of the activity shaded. The thin vertical arrows indicate the time of neural-target selection for each group of trials. The neuron discriminated the target from the distractors after a relatively constant interval after presentation of the search array. The vertical scale represents 100 spikes s^{-1}. (Modified from Sato *et al.* 2001). (*c*) The time of saccade initiation is specified by the activation of another population of neurons. This population may or may not have a visual response, but the neuron saccades are initiated when the activation in a different pool of neurons reaches a threshold. These neurons may or may not have a visual response, but they do discharge in a manner sufficient to control whether and when a saccade will be produced. The variability of saccade latency can be accounted for by randomness in the time taken by the premovement activity to reach the threshold.

superior colliculus (Ottes *et al.* 1987; Basso & Wurtz 1998) and posterior parietal cortex (Gottlieb *et al.* 1998; Contantinidis & Steinmetz 2001). The selection of the target expressed by visuomotor structures such as the FEF is surely related to, if not based on, the selection process observed in the extrastriate visual cortex (e.g. Chelazzi *et al.* 1993, 1998; Motter 1994*a*,*b*; Luck *et al.* 1997).

The result does not distinguish whether this selection process corresponds to explicit visual selection or to saccade preparation. A series of experiments has been conducted to evaluate these alternative hypotheses. In one study, FEF activity was recorded while monkeys maintained fixation during the presentation of a search array with a single conspicuous oddball (Thompson *et al.* 1997). Although no saccade was made to the oddball, FEF neurons still discriminated the oddball from distractors at the same time and to the same degree as when a gaze shift was produced (figure 4*b*). Thus, the visual selection observed in the FEF does not require saccade execution. This study also concluded that saccade preparation was not happening because the saccade made after the trial was completed was rarely directed to the location where the oddball had been. Another experiment created a condition in which monkeys frequently shifted their gaze to a location different from that occupied by a target. Even when the gaze shifted away from the pop-out oddball of a search array, visual neurons in the FEF represented the current location of the target (Murthy *et al.* 2001). Given the evidence that attention is allocated automatically to the conspicuous oddball in a search array, these findings are consistent with the hypothesis that the activation of visually responsive neurons in the FEF corresponds to or guides the covert orientating of visual attention.

Further evidence for the dissociation between neural selection of the target by FEF neurons and the production of saccades was obtained by analysing the time needed by FEF neurons to locate the target in relation to saccade latency. This work is motivated by the general hypothesis that behavioural response times are occupied by more or less distinct stages of processing (Donders 1868; Sternberg 1969). A series of studies has investigated how the time of visual target selection relates to the total time taken to initiate the saccade. During the search for a single, conspicuous target in a search array the large majority of visually responsive neurons in the FEF discriminated the target from distractors at a constant interval after a

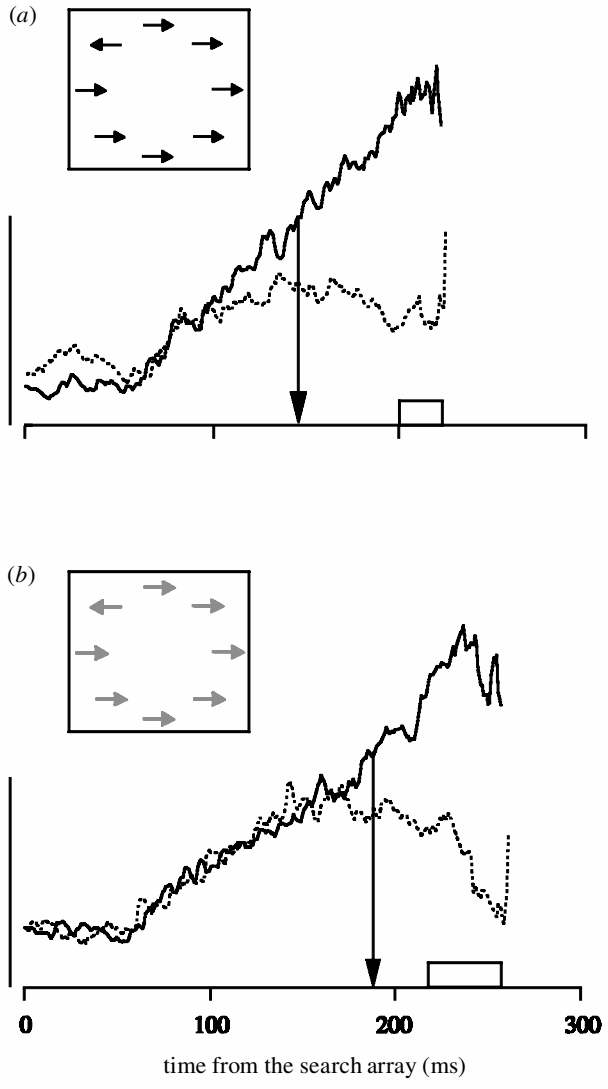

Figure 6. Effect of search difficulty on the time course of target selection. Activity of a FEF neuron during interleaved trials searching for a target that was easy (*a*) or difficult (*b*) to distinguish from the distractors. The neural selection of the target is delayed in the difficult search. (Modified from Sato *et al.* 2001.)

search-array presentation (Thompson *et al.* 1996; Sato *et al.* 2001; figure 5). This finding indicates that at least under the conditions of a efficient, pop-out search, a relatively constant period of time is needed to locate potential targets, and the additional variability in saccade latency is introduced by the time to prepare and execute the eye movement. When the discrimination of the target is more difficult because the target more closely resembles distractors and the search is less efficient (Duncan & Humphreys 1989; Wolfe 1998), the time taken by FEF neurons to locate the target increases and accounts for a larger fraction of the variability in saccade latency (Bichot *et al.* 2001*b*; Sato *et al.* 2001; figure 6).

4. CONTROL OF SACCADE INITIATION

The results just reviewed indicate that certain neurons in the FEF produce a signal that specifies the location of a target for a saccade but does not dictate when or even necessarily where the eyes will move. As described in § 2, a population of neurons in a network including the FEF and superior colliculus linked through the basal ganglia and thalamus provide the input to the brainstem saccade generator. The activation of these neurons is necessary to produce a saccade; therefore, it is appropriate to identify response preparation with the activation of these presaccadic, movement neurons (also referred to as build-up neurons or prelude neurons). Saccades are initiated when the level of activation in this network reaches a certain level (Sparks 1978; Hanes & Schall 1996; Dorris & Munoz 1998). The timing variability of saccade latency is accounted for by randomness in the time needed for the presaccadic activity to reach the triggering threshold. The variability in the time taken to reach the threshold can originate in the time of onset and in the rate of growth of the activation. The growth of movement activity begins at a fixed interval after the appearance of a visual target for a speeded saccade, but under conditions with less clear targets (e.g. Thompson & Schall 2000) or imposed delays (e.g. Riehle & Requin 1993), the beginning of movement activity can occur at a more variable time. Most of the variability of saccade latency in a direct response to a visual target was accounted for by randomness in the rate of growth of activity to the threshold (Hanes & Schall 1996; figure 5*c*).

To investigate the neural control of movement initiation, we have implemented a behavioural paradigm with monkeys, referred to as the countermanding paradigm, which was originally designed to investigate human performance (Logan & Cowan 1984). The countermanding paradigm probes a subject's ability to control the production of movements in a reaction-time task that infrequently presents an imperative 'stop signal'. In the oculomotor version, monkeys were trained to make a saccade to a peripheral target unless a stop signal was presented, in which case they must withhold the movement; the stop signal was the reappearance of the fixation spot (Hanes & Schall 1995; Hanes & Carpenter 1999) or another kind of stimulus (Cabel *et al.* 2000).

Performance on this task can be accounted for by a race between a process that generates the movement and a process that inhibits the movement (Logan & Cowan 1984). This race model provides an estimate of the time needed to cancel the planned movement, the stop-signal reaction time. Oculomotor stop-signal reaction times average *ca.* 100 ms in monkeys (Hanes & Schall 1995) and are slightly longer in humans (Hanes & Carpenter 1999; Cabel *et al.* 2000).

The countermanding paradigm provides experimental leverage such that one can determine whether single neurons generate signals that are sufficient to control the production of movements. The logic of the countermanding paradigm establishes two criteria that a neuron must meet to play a direct role in the control of movement. First, the neuron must discharge differently when a saccade is initiated versus when a saccade is withheld. Second, the difference in activity must occur within the time that the movement is cancelled as measured by the stop-signal reaction time. This approach was applied to neural activity recorded in the FEF (Hanes *et al.* 1998). The first main finding was that movement-related activity in the FEF, which began to grow towards the trigger threshold, failed to reach the threshold activation when movements were

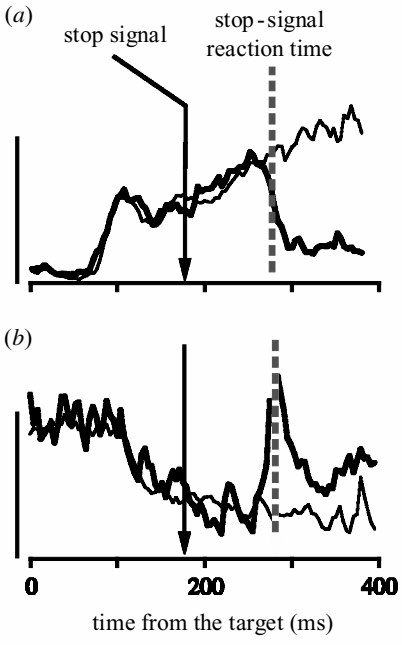

Figure 7. Relationship between the FEF activity and cancelling a movement. (*a*) Activity of a movement neuron in the FEF in trials in which the movement was produced but would have been cancelled if the stop signal had been presented (thin line) is compared with activity on trials when the planned saccade was cancelled because the stop signal appeared (thick line). The time of the stop signal is indicated by the solid vertical arrow. The time needed to cancel the planned movement, the stop-signal reaction time, is indicated by the dashed vertical line. The activity when the movement was cancelled decayed immediately before the stop-signal reaction time. (*b*) Activity of a fixation neuron in the FEF when saccades were initiated (thin line) or cancelled (thick line). The time of the stop signal is indicated by the solid vertical arrow. The time needed to cancel the planned movement, the stop-signal reaction time, is indicated by the dashed vertical line. The activity when the movement was cancelled increased immediately before the stop-signal reaction time. The vertical scale bar marks 100 spikes s^{-1} (modified from Hanes *et al.* 1998).

cancelled but instead decreased rapidly after the stop signal was presented (figure 7). Likewise, fixation-related activity in the FEF, which began to decrease before the saccade, increased rapidly after the stop signal was presented. Moreover, the modulation of the movement- and fixation-related activity differentiated between execution and inhibition of the movement before the stop-signal reaction time had elapsed. Therefore, according to the logic of the countermanding paradigm, the activity of these neurons was sufficient to specify whether or not the saccade would be produced. The same result has been observed in the superior colliculus (Hanes & Paré 1998).

By contrast, most neurons with visual responses but no saccade-related activity exhibited no modulation associated with cancelling the planned movement and those that did were modulated well after the stop-signal reaction time, too late to make any difference to gaze control. These results indicate that distinct types of neurons can be identified that convey signals related more exclusively to visual processing or to saccade production. The distinction between these different pools of neurons provides the basis for different stages of processing and the according flexibility in mapping responses onto stimuli.

5. SELECTION OF A TARGET REQUIRING KNOWLEDGE

Several lines of evidence demonstrate that gaze can be guided as much by knowledge as by the visual features of stimuli. For example, cognitive strategies can override both covert (e.g. Bacon & Egeth 1994) and overt (e.g. Bichot *et al.* 1996) selection of a single oddball in a search array. Also, target selection is influenced by implicit memory representations arising through short-term priming of location or stimulus features for covert (e.g. Maljkovic & Nakayama 1994, 1996) and overt (Bichot & Schall 1999*b*; McPeek *et al.* 1999) orientating. In addition, experts are more likely than novices to ignore conspicuous but irrelevant parts of a visual image from their field of expertise (e.g. Nodine *et al.* 1996; Chapman & Underwood 1998; Nodine & Krupinski 1998). Finally, the pattern of visual fixation can be influenced by verbal instructions (Yarbus 1967). This means that selection of targets for gaze shifts can be influenced by experience.

To study the effects of training experience on gaze behaviour and associated neural activity in the FEF, monkeys were trained exclusively with search arrays that contained a single item of a constant colour among distractor items of another constant colour (e.g. always a red target among green distractors or always a green target among red distractors; Bichot *et al.* 1996). Control monkeys were trained to shift their gaze to the oddball of both configurations of the search array (i.e. alternating between red among green and green among red). The control monkeys shifted their gaze to the oddball stimulus, regardless of the feature that defined it. By contrast, experimental monkeys persistently directed their gaze to stimuli with the colour of the target even when the configuration of the array was switched for a few trials. In other words, when the experimental monkeys were presented with the search array complementary to that with which they had been trained, they shifted gaze to one of the distractors (that was the colour of the over-learned target) and not to the target (even though it was the oddball). As described, FEF neurons in control monkeys did not exhibit feature selectivity, but their activity evolved to signal the location of the oddball stimulus. In monkeys trained exclusively with a search array with constant target and distractor colours, however, about half of the FEF neurons became colour selective. That is, if the over-learned target fell in the receptive field the neurons responded strongly, but if the over-learned distractors fell in the receptive field the neurons' response was significantly weaker or absent. This gives rise to the question of how this initial selective response might arise in the FEF. One possibility is that appropriate bias signals are delivered to the FEF from prefrontal areas. Other studies have demonstrated that the selective properties of prefrontal neurons can change according to rules or strategies (e.g. White & Wise 1999; Wallis *et al.* 2001).

Knowledge gained through experience is necessary when objects of interest cannot be located based only on their visual features. Such cases are exemplified by a visual search for a conjunction of features such as colour and shape in which an explicit memory representation is

needed to identify the target (e.g. Treisman & Sato 1990). A recent study investigated how the brain combines knowledge with visual processing to locate targets for eye movements by training monkeys to perform a visual search for a target defined by a unique combination of colour and shape (e.g. red cross). The colour–shape combination that defined the target were rotated randomly between sessions. Two separate, contextual influences were exerted on gaze behaviour and the neural-selection process: visual similarity to the target and the history of target properties (Bichot & Schall 1999*a*,*b*). The evidence for the influence of visual similarity was that monkeys made occasional errant saccades during this conjunction search that tended to direct their gaze to distractors that resembled the current target. Similar observations have been made with human observers during covert (Kim & Cave 1995) and overt orientating (Findlay 1997; Motter & Belky 1998).

When monkeys successfully shifted their gaze to the target, FEF neurons not only discriminated the target from the distractors but also discriminated among the non-selected distractors resulting in more activation for distractors that shared a target feature than for distractors that shared none (figure 8). Thus, the pattern of neural discrimination among non-selected distractors corresponded to the pattern of errors that reveal the allocation of attention. Evidently, a template of the target held in memory influenced performance and activity.

During conjunction search, the history of stimulus presentation across sessions also affected the selection process. If an error was made, monkeys showed a significant tendency (in addition to the visual similarity tendency just described) to shift their gaze to the distractors that had been the target in the previous session. Recordings from FEF neurons during trials with correct saccades to the conjunction target revealed a corresponding discrimination among distractors with more activation for distractors that had been the target during the previous session. This effect was evident across sessions that were more than a day apart and persisted throughout the experimental sessions. The longer duration of this influence distinguishes this learning effect from the short-term priming during pop-out searches that lasts for about 10 trials or 30 s in humans (Maljkovic & Nakayama 1994; McPeek *et al.* 1999) as well as monkeys (Bichot & Schall 1999*b*).

The source of this contextual modulation observed in the FEF is not known. Recent findings have prompted the suggestion that dorsolateral prefrontal cortex encodes rules for guiding behaviour (e.g. White & Wise 1999; Wallis *et al.* 2001). The activity of neurons in dorsolateral prefrontal areas rostral to the FEF has been described during visual searching (Rainer *et al.* 1998; Hasegawa *et al.* 2000), but the selection was more 'all or none' because the responses began after the selection process was completed. Thus, under these search conditions non-target stimuli did not activate cells in the prefrontal areas 12 and 46. Much more research is needed to understand how arbitrary rules influence saccade target selection.

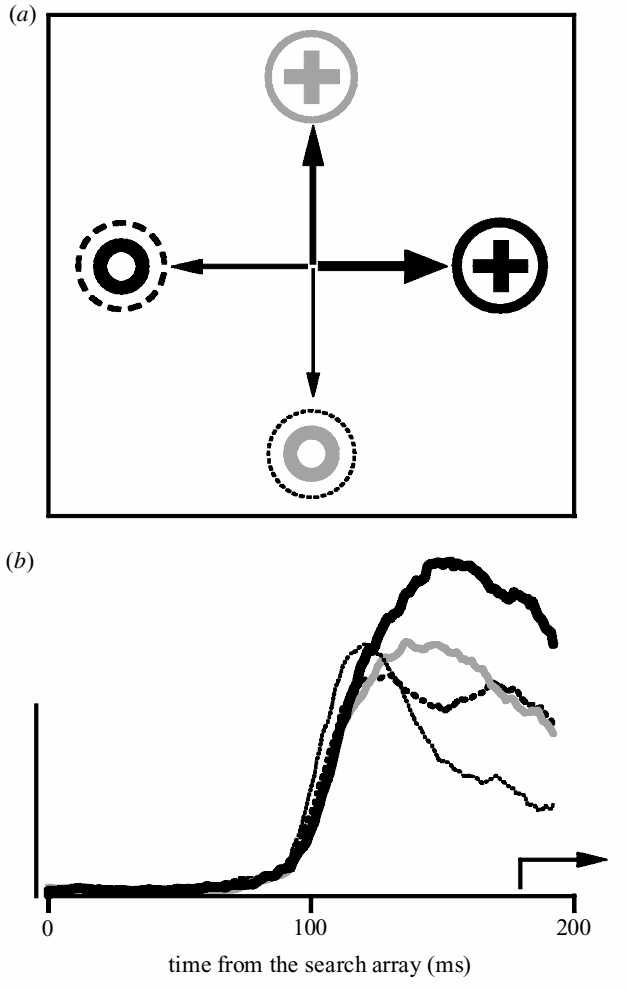

Figure 8. The visual selection of a remembered target during a conjunction search. The assignment of the patterns of neural activation and the incidence of saccades to the alternative stimuli is indicated in the upper diagram of the search array. (*a*) The width of the arrows in the search array represents the incidence of saccades to the different stimuli. Most saccades were made to the target (black cross). Occasional errant saccades were directed to distractors that were the same shape or colour as the target (black circle, grey cross) more often than to the distractor that shared neither feature with the target (grey circle). In addition, errant saccades exhibited an additional tendency to shift the gaze to the distractor that had been the target in the previous experimental session (grey cross). (*b*) The evolution of activity of a FEF neuron is shown during conjunction search when the target stimulus (black solid line), same-colour distractors (dashed line), same-shape distractors (grey line) and the opposite distractors (dotted line) fell in the receptive field. The range of saccade latencies to the target is indicated on the abscissa. The initial response did not distinguish the target from the various kinds of distractors but the activation for the target rapidly became greater, while the activation for the distractors was reduced. The degree of suppression of the distractor activation varied according to whether the distractors resembled the target or had been the target in the previous session. The vertical scale bar marks 50 spikes s^{-1}. (Modified from Bichot & Schall 1999*a*.)

6. CONCLUSION

The picture that emerges from these experiments is that the visual-selection process occupies a certain amount of time. The activation leading to a saccade-movement activity begins to grow as the selection process is completed and (for reasons that are not clear) the rate of

growth of activity leading to the movement varies such that sometimes the gaze shifts sooner and sometimes the gaze shifts later. Due to the delayed and variable growth of the pre-movement activity, the occurrence of a subsequent stimulus can result in adaptive cancellation of the original saccade. Evidence from many studies of event-related potentials also supports the validity of partitioning reaction time into perceptual and response periods (reviewed by Coles *et al.* 1995).

These two stages—visual selection and response preparation—are distinct and only loosely coupled. The variability of fixation duration described earlier can be explained by variation in the movement preparation process independent of the visual-selection process. In fact, it is possible for the saccade-preparation process to become activated before identification of the currently fixated element and selection of the next target are completed. For example, during visual-search movement neurons with no visual response in the FEF can exhibit partial activation for non-target stimuli that resemble the target (Bichot *et al.* 2001*a*). Indeed, the excessive activation of movement neurons can result in premature, erroneous saccades such as those illustrated in figure 1. The independence of visual selection and response preparation is also necessary to explain the production of saccades that are not directed to the location of the selected target. For example, it is possible to withhold a saccade or even to shift the gaze in the direction opposite to a visual target (Hallett & Adams 1980). In monkeys producing antisaccades, visually responsive neurons in the FEF or superior colliculus respond if the target falls in the receptive field and the movement neurons are active for saccades into the movement field if it is a pro- or an anti-saccade (Everling *et al.* 1999; Everling & Munoz 2000).

To summarize, the evolution of visually evoked activity in the FEF represents the process and outcome of the selection of targets for orientating. This selection process can represent not only the target for an overt gaze shift but also the location of a covert attention shift. Clearly, the visual selection observed in the FEF depends on afferents conveying feature selectivity from the various visual areas. However, recall that the FEF provides extensive feedback connections to the extrastriate visual cortex (Baizer *et al.* 1991; Schall *et al.* 1995*b*; Barone *et al.* 2000) and so we should not overlook the possibility that the state of neural activity in the FEF can influence neural processing in the extrastriate visual cortex. The distinction between visual processing and selection and movement preparation and execution is warranted by neural data and necessary to explain the arbitrary and flexible guidance of movements by vision.

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GLOSSARY

FEF: frontal eye field