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Neural mechanisms of selection and control of visually guided eye movements

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Abstract

The selection and control of action is a critical problem for both biological and machine animated systems that must operate in complex real world situations. Visually guided eye movements provide a fruitful and important domain in which to investigate mechanisms of selection and control. Our work has focused on the neural processes that select the target for an eye movement and the neural processes that regulate the production of eye movements. We have investigated primarily an area in the frontal cortex that plays a central role in the production of purposive eye movements which is called the frontal eye field. A fundamental property of biological nervous systems is variability in the time to respond to stimuli. Thus, we have been particularly interested in examining whether the time occupied by perceptual and motor decisions explains the duration and variability of behavioral reaction times. Current evidence indicates that salient visual targets are located through a temporal evolution of retinotopically mapped visually evoked activation. The responses to non-target stimuli become suppressed, leaving the activation representing the target maximal. The selection of the target leads to growth of movement-related activity at a stochastic rate toward a fixed threshold to generate the gaze shift. For a given image, the neural concomitants of perceptual processing occupy a relatively constant interval so that stochastic variability in response preparation introduces additional variability in reaction times. Neural processes in another cortical area, the supplementary eye field, do not participate in the control of eye movements but seem to monitor performance. The signals and processes that have been observed in the cerebral cortex of behaving monkeys may provide useful examples for the engineering problems of robotics. © 1998 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Eye movements are necessary for vision. While this is true for all sighted creatures, it is especially so for primates that possess a focus of high acuity vision called the fovea. Vision is accomplished through an unceasing cycle of fixations and gaze shifts because it is necessary to direct the focus of gaze on different parts of a complex real-world image because visual acuity declines rapidly with increasing distance from the fovea. As a matter of fact, primates make more than 100 000 eye movements every day.

Fig. 1 illustrates the pattern of eye movements made by a monkey searching for a randomly oriented **T** among randomly oriented **L**s. The rapid shifts of gaze from one object to another are called saccades. Saccades tend to direct gaze to conspicuous, informative elements in the image. If subjects are looking for a particular object, then gaze focuses primarily on appropriate elements in the image; otherwise, gaze is dispersed (e.g. Yarbus, 1967; Viviani, 1990). Recent studies in which eye, head and hand movements are recorded while subjects perform simple tasks have shown systematic relationships between gaze behavior and information acquisition for visually guided behavior (e.g. Ballard et al., 1995). Behavior of this sort indicates that before each saccade the brain selects the target for the eye movement. Deciding where to look represents the outcome of visual processing and cognitive guidance. The neural systems responsible for visual processing have been described (Colby and Duhamel, 1991; Merigan and Maunsell, 1993), as have neural correlates of visual perception (Parker and Newsome, 1998) and attention (Desimone and Duncan, 1995; Maunsell, 1995; Schall, 1995; Schall and Bichot, 1998). In the first half of this review, we will discuss the new evidence from our laboratory on neural correlates of saccade target selection in frontal eye field.

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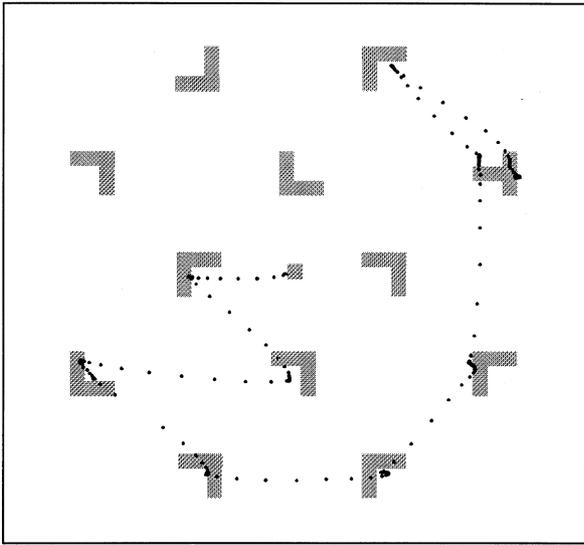
Fig. 1. Pattern of gaze shifts made by a monkey searching for a randomly oriented **T** among **L**s. The **T** among **L** array appeared after the monkey was fixating the central spot. On this trial the monkey's first saccade was to the left, followed by a sequence of eye movements around the perimeter of the array.

During each saccadic eye movement vision is in essence shut down. The reader can be convinced of this by looking in a mirror and shifting gaze from one eye to the other and back again. One will find it effectively impossible to see one's own saccadic eye movements. This saccadic suppression is due in part to image motion and masking effects, but active neural processes play some role (reviewed by Matin (1974)). The influence of saccadic suppression begins as much as 100 ms before and lasts as long as 100 ms after a saccade. So while we must move our eyes to see, if we move them too much, we will be effectively blind. The balance between gaze holding and gaze shifting requires a brain system to regulate the production of eye movements over time. Deciding when to shift gaze is the province of the oculomotor system (Wurtz and Goldberg, 1989; Carpenter, 1991). In the second half of this review, we will discuss new insights into how cortical neural processes regulate the initiation of eye movements.

Why investigate eye movements? Will what is learned about the perceptual and motor decisions associated with visually guided saccades be applicable to other sensory systems and the skeletal motor system? We believe that the knowledge gained about the high level control of eye movements will indeed provide more general insights. In fact, the study of the production of visually guided eye movements provides a number of advantages. In terms of kinematics, the rotation of the eye in Listing's plane is much simpler than movement of multijointed limbs with many degrees of freedom. In terms of dynamics, movements of the eyes floating nimbly in the orbits do not entail the complex torques that occur with limb movements. Moreover, the questions we will address about target selection and the control of movement involve processes that

probably generalize across motor systems. In fact, a number of lines of behavioral evidence indicate that the high level control of gaze operates according to similar principles as the high level control of limb movements or speech. For example, when asked to generate a sequence of saccades, the latency of the first saccade increases with the number of movements in the sequence (Zingale and Kowler, 1987) following the same pattern observed for speech and typing (Sternberg et al., 1978). This is just one example among many which demonstrates that the high-level programming and behavioral control of eye movements seems indistinguishable from that of manual movements or even speech.

2. Frontal eye field (FEF)

The FEF is an area in the prefrontal cortex, located in the rostral bank of the arcuate sulcus of macaques. Broadly considered, this cortical area participates in the transformation of visual signals into saccade motor commands (reviewed by Schall (1997)). As illustrated in Fig. 2, the FEF is innervated in a topographic fashion by areas in both the dorsal and ventral streams of extrastriate visual cortex (e.g. Schall et al., 1995b). The part of the FEF that is responsible for generating short amplitude saccades receives visual afferents from the foveal representation in retinotopically organized areas such as MT and V4, from areas that represent central vision in inferotemporal cortex such as TEO and caudal TE and from areas in parietal cortex having little retinotopic order such as LIP. In contrast, the portion of the FEF that is responsible for generating larger amplitude saccades is innervated by the peripheral visual field representation of retinotopically organized areas, from areas that emphasize peripheral vision such as MSTd and PO, as well as from LIP. The FEF is also innervated by areas in the prefrontal cortex (Stanton et al., 1993).

As a result of this extensive connectivity with extrastriate visual cortical areas, many neurons in the FEF respond to visual stimuli. Physiological recordings in the FEF of monkeys trained in visual tracking tasks have found that roughly half of the neurons have visual responses (e.g. Mohler et al., 1973; Bruce and Goldberg, 1985; Schall, 1991b). Unlike neurons in other visual cortical areas, the responses of the FEF neurons are not selective for the features of stimuli such as color, form or motion. The FEF receptive fields are localized, emphasizing the contralateral hemifield but occasionally extending into the ipsilateral. The visual responses of many FEF neurons exhibit profound extraretinal modulation. As previously observed in the superior colliculus, the response of the visual cells is enhanced if the stimulus is the target for a saccade (Goldberg and Bushnell, 1981). This enhancement occurs specifically for stimuli in the receptive field of the neuron that the monkey is going to look at.
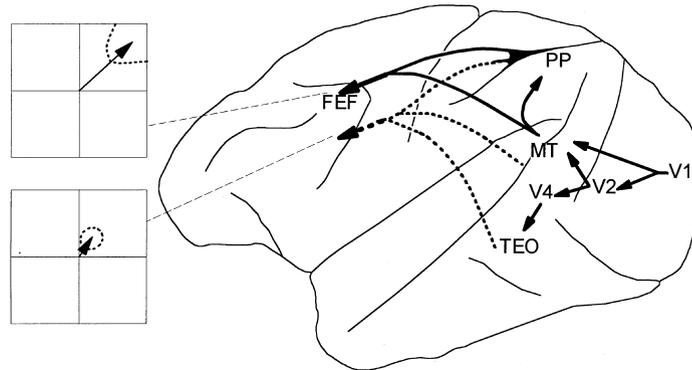
Fig. 2. Pattern of visual afferents to the FEF in macaques. A lateral view of a macaque cerebral cortex shows the location of particular visual and visuomotor areas. Rostral is to the left, dorsal, to the top. Visual processing in the cortex begins in primary visual cortex (V1) from which issue two streams of processing. One stream, responsible for form and object recognition, proceeds into the inferior temporal lobe through areas V2, V4 and TEO. Neurons in and around area TEO respond selectively according to visual color or form. The second stream, responsible for guiding action in space, proceeds into the posterior parietal (PP) cortex through area MT among other areas. Neurons in MT respond best to moving visual stimuli, signaling the direction of motion. Neurons in the posterior parietal cortex represent the location and motion of stimuli needed to guide accurate movements. The FEF is located in the prefrontal cortex. Saccade amplitude is mapped in the FEF as indicated by the insets; ventrolateral FEF generates shorter saccades, and progressively longer saccades are generated by dorsomedial FEF. The part of the FEF that generates longer saccades receives inputs from parts of MT and associated areas that represent peripheral vision and from the posterior parietal cortex. The part of the FEF that generates shorter saccades receives inputs from areas in the caudal temporal lobe, from parts of MT that represent central vision and from the posterior parietal cortex. Thus ventral FEF is one site of convergence of the two visual processing streams.

The anatomical evidence that the FEF receives inputs from multiple visual areas representing various stages and kinds of processing coupled with the physiological evidence that will be reviewed below indicate that it may be useful to regard the FEF at least in part as a saliency map. In many models of visual attention a saliency map is a topographic representation of the visual field in which the locations of potential targets are registered (e.g. Treisman, 1988; Cave and Wolfe, 1990). The activation in the saliency map leads to the particular choice of action. The activation in the saliency map is derived in part from bottom-up processes that identify conspicuous elements in the image defined by the range of elementary features, e.g. color, form, motion, stereo. The saliency map also reflects top-down influences based on goals and expectations.

The activation in the saliency map serves to guide action. Consistent with this, the FEF is well known to play a direct role in producing saccadic eye movements. Low intensity intracortical microstimulation of the FEF elicits saccades (e.g. Bruce et al., 1985). This direct influence is mediated by a subpopulation of neurons in the FEF that discharges specifically before and during saccades (Bruce and Goldberg, 1985; Hanes and Schall, 1996). These neurons that generate movement-related activity innervate the superior colliculus (Segraves and Goldberg, 1987) and the brainstem saccade generating circuit (Segraves, 1992). Recent work has demonstrated that reversible inactivation of the FEF impairs monkeys' ability to make saccades (Dias et al., 1995; Sommer and Tehovnik, 1997) and complements earlier observations that ablation of the FEF causes an initial severe impairment in saccade production that recovers over time (e.g. Schiller et al., 1987).

3. Neural correlates of saccade target selection

3.1. Target selection in the FEF

To investigate how the brain selects the target for an eye movement, a choice must be provided. This can be accomplished by presenting more than one stimulus at a time, with one being visually distinct from the others. For many years, visual selection and attention in humans have been investigated using the visual search paradigm (reviewed by Treisman (1988) and Egeth and Yantis (1997)). Macaque monkeys also will learn very quickly to direct gaze to the oddball stimulus among similar distractors. To investigate how the brain selects targets for visually guided saccades, our colleagues and we have recorded the activity of neurons in the FEF of monkeys trained to shift gaze to the oddball target in either of two complementary pop-out visual search arrays (Fig. 3) (Schall et al., 1995a; Bichot et al., 1996; Thompson et al., 1996, 1997). The initial visual response of most visually responsive cells in the FEF did not discriminate whether the target or the distractor of the search array was in their receptive field (Fig. 3) (but see Bichot et al. (1996)). However, before saccades were generated, a discrimination process proceeded by which most visually responsive cells in the FEF ultimately signaled the location of the oddball target stimulus. The target discrimination was achieved by a suppression or decay of the responses evoked by the distractor associated with a maintenance or enhancement of responses evoked by the target. The magnitude of the distractor suppression in some cells reflected the proximity of the target to the receptive field, there being more suppression of the response to the distractor centered in the receptive field if the target flanked the receptive field.
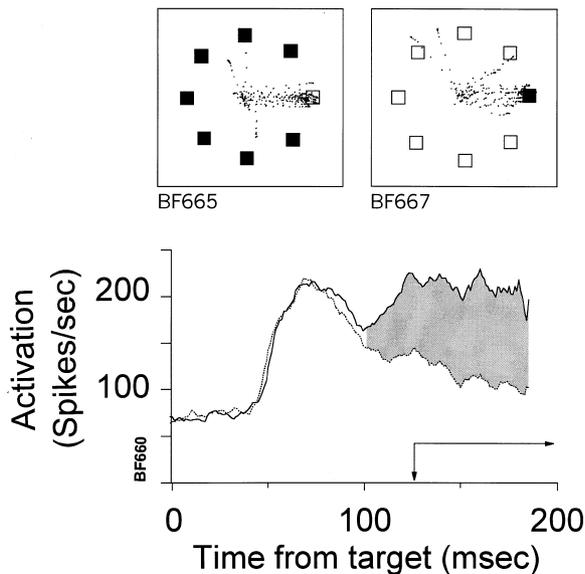
Fig. 3. Visual target selection in the FEF. The top panels illustrate the saccades made by a monkey in response to complementary visual search arrays. The bottom panel shows the time course of activation of a single FEF neuron during the visual search task when the target was in the receptive field (solid line) and when distractors were in the receptive field (dotted line). The arrows indicate the period in which saccades were produced and the filled region indicates the interval when the two curves were significantly different. (Modified from Thompson et al., 1996.)

This center-surround organization of the visual selection observed in the FEF is reminiscent of the receptive field organization observed in other cortical areas and subcortical structures (e.g. Allman et al., 1985).

Does the activity of FEF visual neurons contribute to the visual discrimination, or does it merely reflect the state of processing conveyed by visual afferents over time? The selection process observed in the FEF may result from intrinsic processing but is most likely derived from the visual cortex afferents that innervate the FEF. Many studies have demonstrated visual selection processes in various visual cortical areas. Recent studies have demonstrated that neurons in the visual cortex are sensitive to local stimulus irregularities (Knierim and Van Essen, 1992) and texture gradients (Olavarria et al., 1992; Zipser et al., 1996). Such processing would serve to locate conspicuous points in the image. Other studies have shown that instructions of what stimulus property or visual field location to attend modulate the responses of neurons in area V4 (Motter, 1994; Connor et al., 1997; Luck et al., 1997), areas MT and MST (Treue and Maunsell, 1996), inferior temporal cortex (Chelazzi et al., 1993) and posterior parietal cortex (Robinson et al., 1995; Steinmetz and Constantinidis, 1995; Shadlen and Newsome, 1996; Platt and Glimcher, 1997; Gottlieb et al., 1998). Anatomical connections exist for each of these areas to influence FEF neurons. However, the FEF also projects back to the visual areas. This raises the possibility that the modulation of neurons in the extrastriate visual areas may occur because of the FEF influence. For this to be true, though, the FEF neurons

would have to be activated at least as early as the visual cortex neurons. A recent investigation has measured the latencies of the visual responses of neurons in multiple visual areas including the FEF in individual macaques (Schmolesky et al., 1998; see also Nowak and Bullier (1997)). Among other observations, this study found that neurons in the FEF respond to light at the same time as do neurons in areas V3, MT and MST. Moreover, at the instant when 50% of the FEF neurons have responded to a visual stimulus (around 70 ms), 25% of the neurons in V1 have yet to respond. This unexpected finding seriously challenges hypotheses of visual system function based on sequential processing through a hierarchical network. Instead, it appears that processing the image and selecting a target for action are the outcome of concurrent processing throughout the distributed network.

3.2. Duration of saccade target selection

Prior to the mid-1800s it was believed that thought was virtually instantaneous, motivated in part by the introspection that the conscious will to make a movement seemed to coincide with the moment of movement initiation (see Boring (1950)). This point of view was severely challenged by Helmholtz's (1850) discovery that conduction speeds in the nervous system were a modest 50 m s^{-1} or so. Helmholtz's discovery ushered the study of behavior and mental processes into the laboratory through measurements of reaction time. For the last century, although interrupted by shifting scientific paradigms and world wars, experimental psychology has sought to provide an account of the processes that intervene between stimulus and response. This program of research has been framed by the postulate that behavioral response times are composed of stages of processing (Donders, 1868; Sternberg, 1969). Most simply, a perceptual stage identifies and encodes stimuli and a response stage prepares and executes movements. Distinguishing separate stages and determining how their duration relates to reaction time has been a central problem for decades (e.g. Posner, 1978; Luce, 1986; Meyer et al., 1988). This view of cognition relates nicely to the modular design intrinsic to the computational approach to vision (Marr, 1982).

When measured, reaction times are found to be long and variable. It is important to note that the variability of reaction time is not a laboratory artifact. When viewing natural scenes, fixation durations range from 200 ms to as much as 800 ms (Viviani, 1990). Furthermore, reaction time variability is not unique to primates; even the primitive jellyfish exhibits variable reaction times (Yerkes, 1903). With this prelude, then, we can ask why are fixation durations so long and variable? While fixating a point in an image at least two processes take place. First, perceptual processing identifies the object in the fovea and locates the target for the next saccade in the periphery. Second,

response preparation programs the saccade. These two processes occupy time.

Based on human performance, perceptual processing requires at least 100 ms (e.g. Salthouse et al., 1981). Inferences from performance studies indicate that saccade programming requires around 100–150 ms (Lisberger et al., 1975; Becker and Jurgens, 1979; Hanes and Schall, 1995). These estimates of minimal perceptual and response preparation delays do not account for the full range of the variability and length of natural fixation durations. Carpenter (1981; 1988) has called attention to this apparent procrastination, noting that much of the delay and variability of fixation durations may probably be attributed to as yet uncharacterized decision processes.

From this perspective we were interested in relating the time course of the target selection process in the FEF to the time of saccade production. Having found that saccade target selection by the FEF neurons occurred over time (Fig. 3), we performed an analysis to determine when the selection was accomplished (Thompson et al., 1996). By comparing the activity of the FEF neurons on trials when either the target or distractors of the visual search array fell in the receptive field, we measured when the difference in activity elicited by the target and distractors occurred. We then measured this time of target discrimination in subsets of trials with different ranges of saccade latencies. By partitioning the reaction time of monkeys this way, we could examine the sources of the variability of saccade reaction times. We found that most FEF neurons with sustained visual activity selected the target for the saccade a fairly constant interval after stimulus presentation (Fig. 4). In other words, the time when the target of the saccade was identified did not predict the time when the eyes moved.

3.3. Dissociation of visual discrimination in the FEF from response preparation

We performed another study to test more directly the hypothesis that visual discrimination by the FEF neurons was contingent on saccade planning and production (Thompson et al., 1997). In the control condition monkeys made a saccade to fixate the oddball stimulus among colored distractors as described previously. In the experimental condition monkeys were given a no-go signal 500 ms before presentation of the search stimulus array in many blocks of trials and were rewarded for maintaining fixation until the search array disappeared 800 ms later. We found that neurons that discriminated the target of the search array in go trials also discriminated the oddball in no-go trials. Now, a potential problem with this study is that the monkeys may have been covertly planning a saccade to the oddball stimulus but shifted gaze only after the trial was completed. We ruled this out, however, by examining the endpoints of the first saccade monkeys made after the trial was over. During recording from the FEF neurons in the no-go
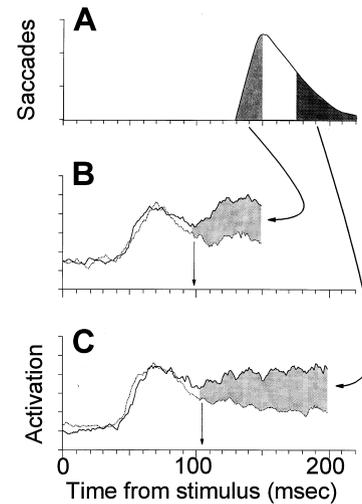

Fig. 4. Relationship between the time of target discrimination in an FEF neuron (B, C) and the time of saccade initiation (A). The time course of activation of a single FEF neuron during the visual search task when the target was in the receptive field (solid line) and when distractors were in the receptive field (dotted line) is shown for subsets of trials in which saccade latency was short (B) or long (C). The times of target discrimination (vertical arrows) were approximately the same in both subsets of trials and, therefore, do not account for the range of saccade latencies.

condition, gaze was not systematically directed to the oddball even after the trial was completed.

These data indicate that visual discrimination by the FEF neurons can occur independently of saccade planning. Human performance studies have shown that attention is automatically drawn to the location of a salient oddball (Theuwees, 1992; Kim and Cave, 1995; Joseph and Optican, 1996; but see Bacon and Egeth (1994)). If attention shifts to the oddball and the FEF neurons discriminate the oddball even though the eyes do not move, then this suggests that the FEF may participate directly in covert visual attention as well as overt gaze shifts. This hypothesis differs from the conclusion reached by earlier investigators who contrasted the visual responses of neurons to visual stimuli that were or were not used to guide movement. Goldberg and coworkers (e.g. Goldberg and Bushnell, 1981) found that visually responsive neurons in the FEF responded more strongly to stimuli that were used as the target for an eye movement compared with stimuli that were presented while the monkey maintained central fixation. The same observation was made in the superior colliculus, and the posterior parietal cortex among other areas. However, neurons in the posterior parietal cortex but not in the FEF or superior colliculus also responded more strongly to stimuli that were just attended but not fixated. In other words, the absence of modulation of the visual responses in the FEF associated with the presumed attention shifts led to the conclusion that the FEF plays a role in directing gaze but not attention. This hypothesis merits reconsideration in light of new evidence. First, human performance studies have demonstrated that although they can be decoupled under certain circumstances

(e.g. Klein et al., 1992), attention and gaze are directed by common mechanisms (e.g. Kowler et al., 1995; Deubel and Schneider, 1996). Second, recent evidence from neuro-imaging studies in humans have suggested that a common zone in the dorsolateral precentral sulcus of frontal cortex is involved in both eye movements and attention (Nobre et al., 1997; Corbetta, 1998).

The observation that the visual discrimination process expressed by visually responsive FEF neurons can occur independently of when or even whether the eyes move demonstrates that the selection process cannot be attributed simply to saccade programming. In the context of the simple visual search task confronting the monkeys, the job of vision is to distinguish and locate the target among the distractors. The signals in the FEF carry that information. Therefore, we suppose that the time course of the neural discrimination process monitored in the FEF corresponds to the time course of the perceptual processing stage. This attribution is a linking proposition (Teller, 1984), a statement relating cognitive and neural processes necessary to develop additional arguments. This hypothesis linking the neural selection process in the FEF to the outcome of perceptual processing must be evaluated experimentally. This can be accomplished by manipulating the visual discriminability of the target relative to the distractors (Thompson et al., 1998) or by using a top-down conjunction search (Bichot and Schall, 1998). If the target selection process in the FEF indexes the evolution of perceptual processing, then the suppression of the responses to the distractors and the time course of the discrimination should be in proportion to the similarity of the distractors to the target.

The premise that the time of target discrimination by the FEF neurons indexes the outcome of perceptual processing, coupled with the fact that the time of saccade initiation was not predicted by the time of target discrimination by the FEF neurons, indicates that variability of response times is not dictated by the duration of perceptual processing. From this we conclude that a significant fraction of the variability in reaction time arises in post-perceptual response preparation. Research using event-related potentials with human performing choice reaction time tasks has arrived at the same conclusion (see Coles et al. (1995)). Therefore, to provide a full account of reaction time in general and saccade latency in particular, it is necessary to consider the response preparation process.

4. Neural control of saccade initiation

4.1. Rise to threshold mechanism for reaction time

Over the years many models have been developed to explain the stochastic variability of reaction time (reviewed by Luce (1986)). Most reaction time models incorporate assumptions that are not physiologically plausible, because such was not their aim. One class of models, though, known as accumulator models, does seem appropriate for evaluation in relation to brain function. Accumulator models suppose that in response to a stimulus, a signal in the brain grows until it reaches a threshold, thereby triggering a motor response to the stimulus. In models of this sort there are at least two sources for the stochastic variability evident in response times. One type of accumulator model supposes that the variability in reaction time arises from randomness in the level of the trigger threshold (e.g. Grice et al., 1982). This model has been shown to account for saccade performance (Nazir and Jacobs, 1991). Another type of accumulator model assumes that the threshold is constant, but the rate of growth of the accumulator is random across trials (e.g. Ratcliff, 1978; Carpenter, 1988). This architecture can also account for reaction time performance (Carpenter and Williams, 1995; Ratcliff et al., 1998). Thus, the two alternative models cannot be distinguished on the basis of performance data alone; indeed, it has been shown mathematically that random accumulator and random threshold models generate equivalent predictions (Dzhafarov, 1993).

We have recently examined movement-related activity recorded in the FEF to evaluate these alternative models of reaction time (Hanes and Schall, 1996). We found that saccades were initiated when movement-related activity in the FEF reached a particular level, but that this threshold level did not vary with saccade latency (Fig. 5). A similar analysis of the amplitude of the lateralized readiness potential, a scalp potential concomitant of movement-related neural activity, led to the same conclusion (Gratton et al., 1988). In the FEF data the variability in reaction time was accounted for by variation in the rate of growth of the premovement activity toward the trigger threshold. Accordingly, the movement-related neural activity in the FEF appears to correspond to an accumulator model
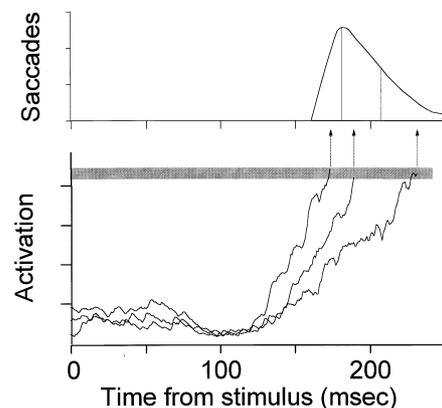

Fig. 5. Relationship between movement-related FEF activity and saccade initiation. Time course of activation of a single movement-related FEF neuron is shown for three subsets of trials having different saccade latencies. Plots are aligned on target presentation and stop at saccade initiation. The level of activity at which the saccade is triggered (gray bar) is fairly constant across saccade latencies. Variability in saccade latency is accounted for by the time taken by the neuron to reach the threshold activation.

architecture with variable growth to a fixed threshold and directly contradicts the architecture with a fixed growth process and random threshold.

An important test of the fixed threshold model was to determine whether the quantitative variation in the rate of growth of the neural activity could account for the actual range of reaction times generated by the monkeys. The distribution of the behavioral reaction times collected while recording from each individual FEF cell was compared with a distribution of reaction times generated by a Monte Carlo simulation run with parameters derived from that neuron's activity. The parameters input to the simulation were derived from the average threshold level and the rates of growth of premovement activation obtained from each neuron individually. The simulated distribution of reaction times was often indistinguishable from the observed distribution of reaction times. Thus, the activity of a single FEF movement neuron appears to be sufficient to account for when movements are produced.

The same relationship between the growth of movement-related neural activity and the time of movement initiation appears to hold for neurons in the motor cortex (Lecas et al., 1986). This evidence indicates a particular architecture for motor response production that includes some random variability. Numerous performance studies have shown that response times can be reduced as conditions become more predictable, but still some proportion of variability remains. Why is the growth of movement-related activity variable? Is it the best possible or the most desirable performance of the system? From a design perspective, random variability may permit more adaptive behavior. The world is an ever-changing place; an action chosen at one instant may in the next become a bad choice. Occasional procrastination may allow the perceptual system to re-evaluate the environment and specify a different action.

These suppositions are based on the validity of the hypothesis that movements are produced when motor activity reaches a fixed threshold. Further research has tested the validity of the threshold conception by comparing neural activity when saccades were either made or withheld after different degrees of preparation.

4.2. The countermanding paradigm

To investigate the neural control of movement production, we have employed a paradigm with behaving monkeys called the countermanding paradigm. Originally developed to investigate human performance, the countermanding paradigm probes a subject's ability to control the initiation of movements in a reaction time task in which an imperative stop signal is infrequently presented (reviewed by Logan (1994)). The subjects' task is to cancel the planned movement if the stop signal is presented. In the oculomotor version (Hanes and Schall, 1995), monkeys were trained to make a saccade to a peripheral target unless a stop signal

was presented, in which case they were to withhold the movement; the stop signal was the reappearance of the fixation spot. Logan and Cowan (1984) showed that 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. This race model provides an estimate of the stop signal reaction time, which is the time needed to cancel the planned movement. Oculomotor stop signal reaction times average around 100 ms in monkeys (Hanes and Schall, 1995) and are approximately 30 ms longer in humans (Hanes and Carpenter, 1998). The stop signal reaction time corresponds theoretically and quantitatively to estimates of the time needed to reprogram a saccade in double-step saccade tasks (Lisberger et al., 1975; Becker and Jurgens, 1979).

4.3. Gaze control signals in the FEF

We applied the countermanding paradigm with the view that one can determine whether single neurons generate signals that are logically sufficient to control the production of movements. The logic of the countermanding paradigm establishes two criteria a neuron must meet if it is to play a direct role in the control of action. First, the neuron must discharge differently when a saccade is initiated versus when a saccade is withheld. Second and most importantly, the difference in activity once the stop signal is presented must occur by the time that the movement is canceled, that is by the time that the stop-signal reaction time elapsed.

Examining neural activity recorded in the FEF, we found that movement-related activity, which began to grow toward the trigger threshold, failed to reach the threshold activation level when movements were canceled (Fig. 6) (Hanes et al., 1998). Instead, when planned movements were canceled,
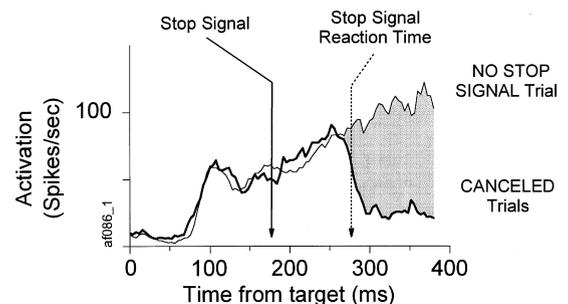
Fig. 6. Movement-related FEF activity when saccades are initiated or canceled. The countermanding task consists of many No Stop Signal trials in which the fixation disappearance and target step is followed by a visually guided saccade. Stop Signal trials occur at random when the target step is followed by the reappearance of the fixation spot (solid vertical line). Stop signal reaction time is the time needed to cancel the planned movement in response to the stop signal (dashed vertical line). The activity on trials in which the movement was produced but would have been canceled if the stop signal had been presented (thin line) is compared with activity on trials when the planned saccade was canceled because the stop signal appeared (thick line). The activity when the movement was canceled decayed precipitously immediately before the stop signal reaction time. (Modified from Hanes et al., 1998.)

the movement-related activity decreased rapidly after the stop signal was presented. Moreover, the movement-related activity associated with inhibition compared with execution of the movement became different before the stop signal reaction time had elapsed. Therefore, according to the logic of the countermanding paradigm, the activity of single FEF movement neurons is logically sufficient to specify whether or not a saccade will be produced. This pattern of results was observed in all cells with movement-related or fixation-related activity, but was never observed in neurons with only visual responses. The different results for the different functional classes of neurons is entirely consistent with the fact that movement and fixation neurons in the FEF directly innervate efferent oculomotor structures but visual neurons do not (Segraves and Goldberg, 1987; Segraves, 1992).

The findings from the countermanding experiment indicate that the preparation of a movement is a controlled process; it can be canceled because the growth of the activation toward the trigger threshold is sufficiently slow. What if errors are made because the movement is not canceled? In the FEF we found no difference in activity associated with movements executed without or in spite of the stop signal. This finding is consistent with the hypothesis that the finish times of the go and of the stop process are independent, which is fundamental to the countermanding paradigm (Logan, 1994). However, to perform the task well, subjects must know when errors are made and adapt their behavior to minimize future errors. Thus, some part of the brain must monitor the consequences of action.

4.4. Performance monitoring by the supplementary eye field (SEF)

We have begun recording neural activity in the supplementary eye field (SEF) in monkeys performing the countermanding task (Patterson and Schall, 1997). The SEF is an area in the dorsomedial frontal cortex that seems in several respects to parallel the FEF. Saccades can be elicited by low intensity microstimulation of the SEF, and neurons in the SEF discharge in relation to saccades (Schlag and Schlag-Rey, 1987; Schall, 1991a, 1991b). The SEF innervates oculomotor centers in the striatum, superior colliculus and brainstem (reviewed in Schall (1997)). These facts might predict that neurons in the SEF ought to behave like their counterparts in the FEF. However, we have found that remarkably few neurons in the SEF generate signals that are sufficient to control gaze according to the logic of the countermanding paradigm. Instead, many neurons in the SEF generate signals as illustrated in Fig. 7.

The neuron shown in Fig. 7 illustrates two of the signals that were observed in the SEF but never in the FEF. This neuron exhibited elevated firing during trials in which the saccade was canceled, but the activity occurred specifically after the stop signal reaction time. This modulation cannot be involved in canceling the movement because it is too
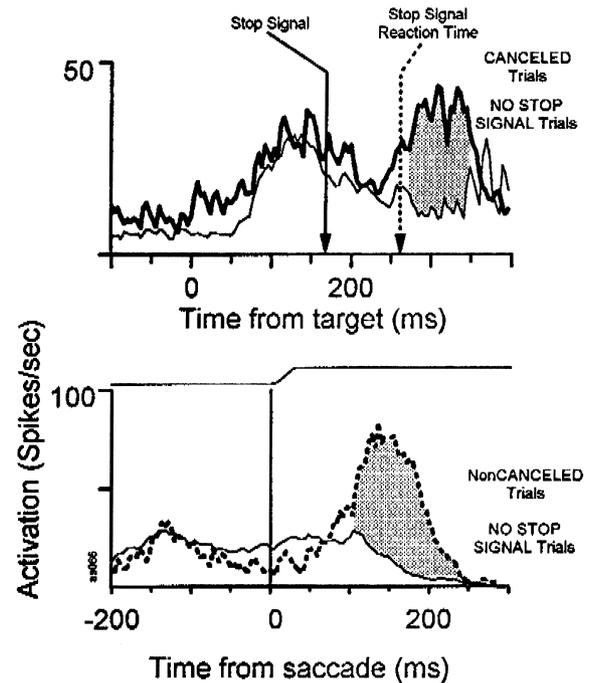

Fig. 7. SEF activity during the countermanding task. The top panel compares the activity between trials when the movement was canceled (thick line) and trials when the movement was produced but would have been canceled if the stop signal had been presented (thin line). The time of the stop signal and the estimated stop signal reaction time are shown. This neuron exhibited a visual response and then was reactivated when the movement was canceled; however, this reactivation occurred after the stop signal reaction time, so it could not have played a role in canceling the movement. The bottom panel compares the activity between trials when the eye movement was made because no stop signal was given (solid line) and trials when the eye movement was made in spite of the stop signal (thick dashed line). This neuron was activated specifically following errant saccades.

late. A speculative hypothesis is that this signal registers successful performance of the task. Such a hypothesis is motivated in part by recent work describing the properties of dopaminergic neurons in signaling rewards (reviewed by Schultz (1997)).

The second signal generated by the SEF neurons occurred specifically in stop signal trials in which the saccade was not canceled. Some SEF neurons discharged after the errant saccade was completed. A speculative hypothesis is that this signal registers the occurrence of an error. This interpretation of the modulation in the SEF is motivated by recent reports of a scalp potential recorded in humans called the error-related negativity (ERN) (Gehring et al., 1993). The ERN occurs only when subjects are aware that they made an error and the magnitude of the ERN predicts the extent to which subjects modify their behavior on the subsequent trial.

The absence of saccade control signals in the SEF is consistent with the fact that following combined ablation of the FEF and the superior colliculus, leaving the SEF intact, monkeys cannot make eye movements (Schiller et al., 1980). The new data from the countermanding paradigm suggest a function for the SEF that distinguishes it from the FEF. The SEF may serve to monitor performance,

registering whether the actions that are produced are appropriate and lead to the desired consequences. Such monitoring seems vital for a self-controlled system that can adapt to changing circumstances. Much more research will need to be done to clarify and evaluate this hypothesis.

5. Conclusion

We have described neural processes that are involved in selecting the target for an eye movement and controlling whether and when the eye movement will be produced. We have also described neural signals that may serve to monitor performance. We expect that the brain signals and processes we have reviewed may provide insights into computational principles that will be useful for non-biological animate systems.

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