Neural Basis of Saccade Target Selection

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SYNOPSIS

This article reviews what is currently known about how the brain selects targets for saccadic eye movements. Saccade target selection is needed because primates can look at just one thing at a time. Target selection ought to be judicious because it is important to look at the right thing in a potentially dangerous and ever changing environment. Usually, conspicuous visual features attract gaze. While much is known about the low level mechanisms responsible for generating saccadic gaze shifts, very little is presently known about how the brain selects the targets for eye movements. Saccade target selection may not be that difficult a problem; there is not yet much neurophysiological data. Current data indicate that when confronted with multiple possible targets, comparisons, possibly through lateral inhibition, are made across the visual field by neurons encoding stimulus features within topographic maps. Through topographic mapping, the outcome of this visual spatial comparison ultimately activates neurons in maps of saccade direction and amplitude that generate a shift of gaze to the desired target and attenuates the activity of cells that would generate inappropriate saccades. Through investigating saccade target selection more can be learned about the roles of structures throughout the visual system as well as elucidating how processes such as attention and memory influence visual processing.

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KEY WORDS

INTRODUCTION

Primate visual behavior is organized around the fovea which provides high acuity vision over a limited range of the central visual field /29/. To identify an object in the scene, the eyes move in conjugate fashion so that the image of the object falls on the fovea. Saccadic eye movements are the rapid shifts of gaze that redirect the visual axis onto a new point in the image. Foveation of an object often precedes further action directed at the object, such as reaching and grasping /16/. During natural viewing, saccades of less than 10° amplitude, which are by far the most common /9/, direct gaze to conspicuous and informative features in the scene /123,172/. Furthermore, when viewing complex images, gaze shifts exhibit idiosyncratic but fairly regular patterns of fixations which have been called scanpaths /112,182/.

Normal visual behavior, thus, is accomplished through a continuous cycle of fixation and visual analysis followed by another fixation and renewed visual analysis; the focus of gaze shifts two to five times every second even when viewing a single object such as a face. This incessant scanning may seem to be unnecessary given that simple or familiar images like faces can be recognized at a glance /15/. Nevertheless, active scanning is what we do, so it is presumably adaptive. In fact, scanning movements have now been used to improve the performance of machine vision systems. A number of the computational problems of early vision are difficult

to solve when using a single image frame but can be solved when the cameras move, that is, when visual processing becomes integrated in ongoing behavior /5,12/. Thus, it seems that further progress in understanding the neural basis of visually guided behavior may require that perception and action be considered together /4,110/. Examination of the physiology and anatomy of the brain force the same conclusion; very few structures in the brain can be assigned exclusively sensory or motor functions. Understanding how the brain selects the targets for saccades will, therefore, involve understanding both visual processing as well as saccade production. After brief surveys of the visual and oculomotor systems, I review the studies that bear more directly on the issue of saccade target selection. A number of brain regions are ignored in this survey because of lack of information rather than lack of involvement in saccade generation.

ORGANIZATION OF THE PRIMATE VISUAL SYSTEM

Work over the last 35 years has produced a detailed knowledge about the organization of the visual system in primates. Two key findings are important for understanding the function of the visual system in selecting features and objects on which to act. First, neurons in the visual cortex respond selectively to stimuli having different features /70/. Second, in the cortex there are multiple representations of the visual field with certain specific functional specializations /36,50/.

Figure 1 portrays a very simplified version of the organization of the visual system in the macaque. Among several targets the retina sends efferents to the dorsal lateral geniculate nucleus (LGNd) and pulvinar in the thalamus and to the superior colliculus. The LGNd relays visual signals to the primary visual cortex (known as area V1). In area V1 the visual field is represented in a precise visuotopic map with neurons having very small receptive fields that increase in size with eccentricity in the visual field. In V1 neurons respond selectively to stimuli differing along several dimensions, including orientation, color and direction of motion. The discrimination of these neurons provides the substrate for

visual selection of stimuli on the basis of different features. Thus, having neurons that respond differently to red versus green spots provides signals that can be used to select just the red or just the green spots for some purpose.

V1 has a number of outputs, both cortical and subcortical. For example, neurons in layer 5 of V1 project to the superior colliculus and confer visual responsiveness on neurons in the deeper layers of the superior colliculus /143/. Within the cortex, V1 projects to at least seven secondary and tertiary regions. It is becoming evident that each of these regions is a separate map of the visual field, encoding somewhat different feature properties or processing attributes. At last count, 32 visual areas were identified in the cortex joined to one another by 305 connections /50/.

Many properties distinguish the various cortical visual areas. For instance, the response properties of neurons vary across areas. Whereas neurons in the middle temporal visual area (area MT, also referred to as V5), situated in the caudal superior temporal sulcus of the macaque, respond preferentially to moving stimuli, neurons in the inferior temporal cortex respond preferentially to objects such as complex stimuli or faces /93,159/. In addition, selective lesions of different areas result in particular visual deficits. Whereas ablations of MT result in a specific deficit in perceiving the speed and direction of moving visual stimuli, ablations of V4 result in deficits in discrimination of hue and pattern and in the selection of the less prominent of several stimuli /68,111,140/. Also, ablations of the posterior parietal cortex result in deficits in behaviors requiring spatial judgments while ablations of the inferior temporal cortex cause deficits in behaviors requiring object recognition /96,167/. Another property that distinguishes cortical areas is that the visual field is mapped differently across areas; whereas in the inferior temporal cortex most neurons have receptive fields emphasizing the fovea and central vision, neurons in the posterior parietal cortex have receptive fields in the peripheral visual field. In fact, whereas certain areas in the visual cortex, such as V1, V4 and MT, have retinotopic maps, the areas exhibiting the extreme overrepresentations of central or peripheral visual field with large receptive fields have no discernible
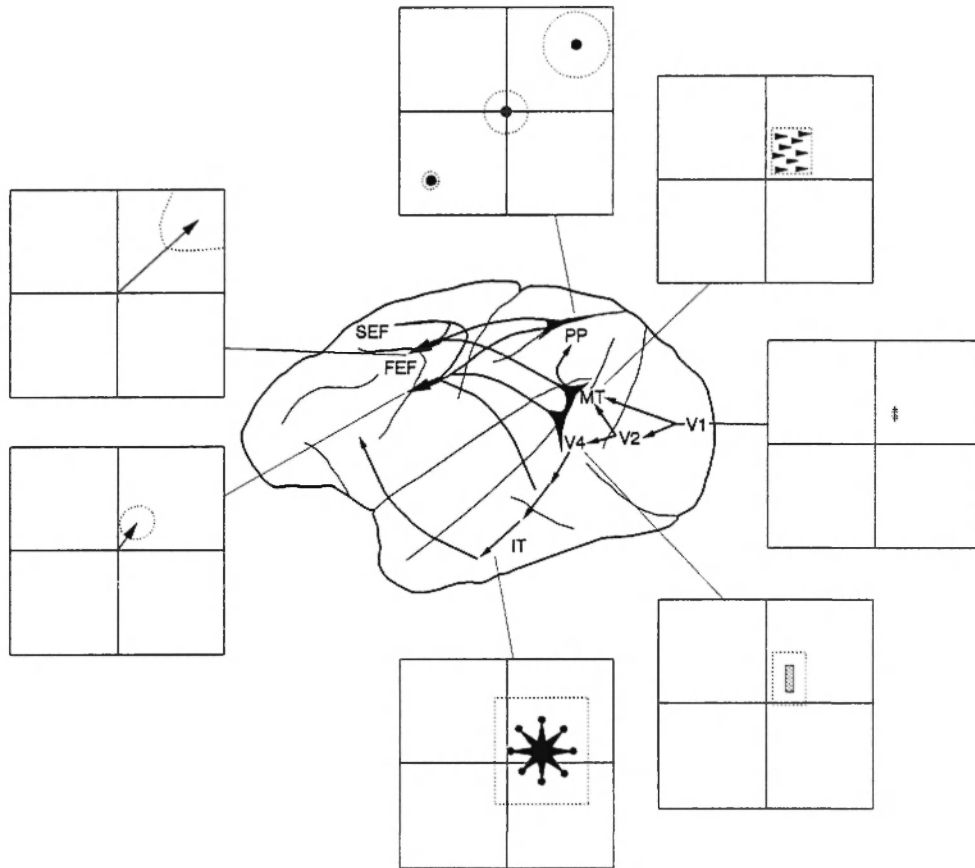
Fig. 1: Simplified overview of macaque monkey cortical visual pathways. The location of the cortical areas described in this review are indicated. Associated with certain areas is a diagram of the visual field with an indication of the basic response property of the neurons in that area. The final stage of processing before each saccade occurs in the frontal eye field (FEF) located in the rostral bank of the arcuate sulcus. Neurons in FEF are visually responsive and discharge in relation to saccades. Whereas neurons in ventrolateral FEF have smaller, central receptive fields (dotted line) and fire for shorter saccades (arrow), neurons in dorsomedial FEF have larger, peripheral receptive fields and fire for longer saccades. Saccade-related activity is also found in the supplementary eye field (SEF), located on the dorsomedial convexity of the cortex, which is reciprocally connected with FEF. Cortical visual processing starts in the primary visual cortex (area V1) where the cells with small receptive fields in a very precise topographic map of the visual fields respond preferentially to stimuli of different orientations, color, direction of motion, stereoscopic depth, etc. (indicated by thin, vertical bar). Efferents from primary visual cortex innervate secondary (V2) and tertiary (e.g., V4, MT) areas from which issue forth many other connections, and the vast network may be organized in at least two streams. One stream passes through area V4 into the inferior temporal (IT) cortex. Neurons in area V4 have larger receptive fields and respond to static stimuli of different orientations or colors (indicated by gray bar); the level of activation of cells in V4 is modulated by visual attention. Area V4 innervates the prearcuate cortex in a topographic fashion. Neurons in caudal IT cortex exhibit less topographic organization than those in V4 but they are still tuned for stimulus features; efferents from this level of IT cortex project mainly to the ventrolateral portion of FEF. In rostral IT cortex neurons are selective for more complex visual objects (indicated by the star shape), including faces. The rostral regions of IT cortex, besides projecting into medial temporal lobe memory circuits, also innervates the ventrolateral prefrontal cortex. This region of prefrontal cortex sends axons into ventrolateral FEF. Thus, FEF itself receives direct visual information about features and indirect information about objects. The second cortical visual processing stream passes through the middle temporal visual area (MT, also referred to as V5) into the posterior parietal cortex (PP). Neurons in MT, also with larger receptive fields, respond best to stimuli moving in one direction (indicated by arrowheads). Neurons in PP cortex exhibit two pronounced extraretinal signals. The first, described in the text, is a modulation of visual responses according to visual attention. The second, illustrated by the variation in apparent receptive field size for different locations, is a modulation of visual responses by angle of gaze. Efferents from PP project throughout the FEF representation of short and long eye movements.

map. Finally, the constellation of intracortical connections supported by each area is different. For example, whereas the inferior temporal cortex is preferentially connected to the foveal representation of retinotopically mapped areas, the posterior parietal cortex is preferentially connected to the peripheral visual field representation of retinotopic areas /11,100/.

Based on the patterns of anatomical connections, investigators have organized the various areas in a hierarchical scheme /6,18,37,50,183/. It is important to realize, though, that visual processing is not sequential, stepping from lower order to higher order areas. Were it sequential, visual response latencies ought to increase from one area to the next. It is the case that response latencies are shortest in V1 /92,106/, ranging as low as 30 ms and up to 100 ms or more. However, although the mean visual response of neurons in the secondary visual area V2 is around 10 ms greater than the V1 average, many V2 neurons have latencies as low as those in V1 /106/. On the other hand, response latencies in the inferior temporal cortex range from as low as 70 ms up to 200 ms /114/. For comparison, visual response latencies in the frontal eye field (FEF) average around 80 ms, ranging from as low as 40 ms to over 100 ms /58,132/. Thus, while activation of many cells in V1 precedes the activation of cells in other areas, the activation of other neurons in V1 begins after neurons in higher visual areas have begun discharging. In general, within 60-100 ms after a stimulus appears almost all visually responsive structures in the brain become active. This simple fact challenges any concrete notion of exclusively serial, sequential processing.

A number of findings have contributed to the view that two distinguishable visual pathways branch out from V1, one passing into the temporal lobe that is responsible for object recognition and the other running into the parietal cortex that is responsible for spatial localization /167,183/. Even though it is becoming clear that there is less segregation and independence than was originally proposed /96/ and that alternative organizing schemes are possible /61/, it is not known precisely how information from the various cortical areas is combined to generate perception and action. Investigations of visually guided eye movements may

provide data with which this question can be examined because information about both object identity and spatial location must be combined to produce accurate eye movements. That is, shorter eye movements are guided by both object and spatial information. However, longer eye movements cannot be guided by sophisticated object recognition processes because of reduced peripheral visual acuity; longer saccades are involved in orienting responses to peripheral visual as well as to acoustic stimuli. Thus, by studying how saccades of different amplitudes are guided by different sorts of visual information, we can get more information to improve our understanding of the roles of different visual areas.

ORGANIZATION OF THE PRIMATE OCULOMOTOR SYSTEM

Figure 2 illustrates a selective overview of some of the major structures of the visuomotor system in primates. A sophisticated understanding of the eye movement production system has emerged over the last 25 years /28,179/. Saccadic eye movements are produced by a pulse of force to initiate the rapid movement combined with a step of force to hold the eye at its new location. A network of neurons in the brainstem is responsible for generating the activation of ocular motor neurons necessary to produce these forces. For our purposes what is important is that activation of a population of *burst* neurons initiates a saccade. These burst neurons are gated by another population of neurons that discharge at a high rate until each saccade. These *pause* neurons tonically inhibit the burst neurons; inhibition of the pause neurons releases the inhibition on the burst neurons thereby permitting production of a saccade. The direction of a saccade is specified by which population of burst cells fire. The amplitude of the saccade is specified by the burst frequency for saccades less than 15° and by burst duration for longer saccades. This network of neurons is so well understood that sophisticated, detailed models have been developed /169/. While the various models may differ in intrinsic details, they share the use of two inputs: where to shift gaze and when to shift gaze.

Thus, the next level of the problem involves specification of which saccade to produce, in other words, producing the conjoint signals of 'where' and 'when'. One key structure innervating the saccade generator is the superior colliculus /128, 152/. The superior colliculus is organized with a topographic representation of visual space in its superficial layers and of saccade movement direction and amplitude in its deeper layers.

The functional properties of visually responsive neurons in the retinotectal system are substantially different from those in the retinogeniculate system.
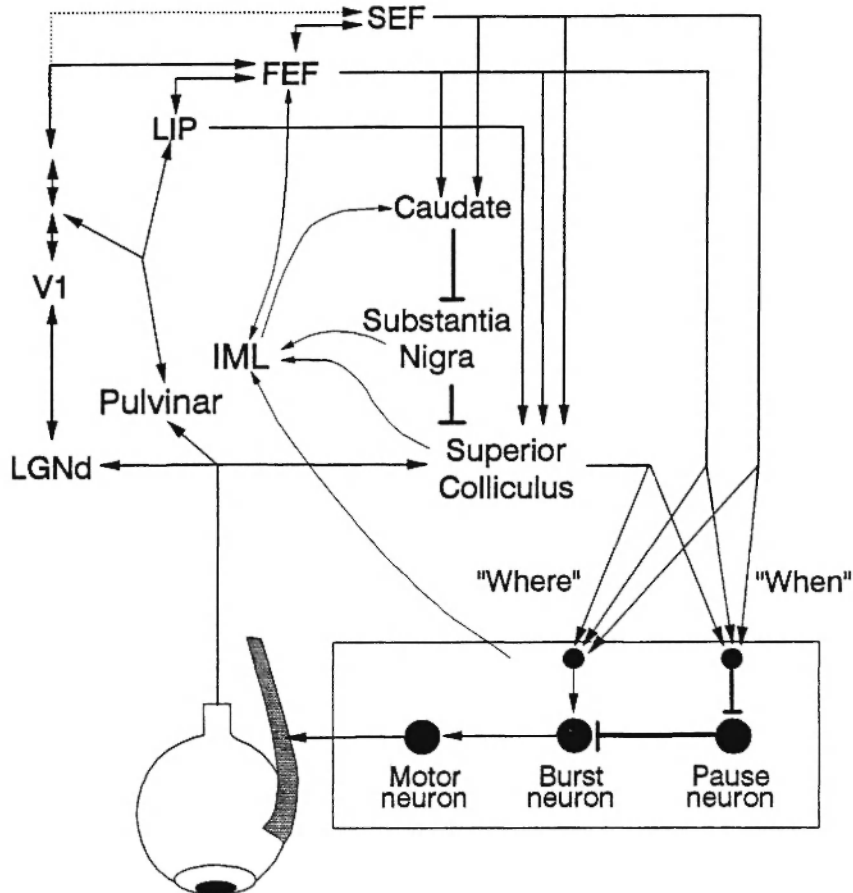

Fig. 2: Summary of the saccade generating network. The diagram illustrates a simplified schematic of the connectivity between structures involved in generating saccadic eye movements. A network located in the brainstem is responsible for generating saccadic eye movements. A saccade is initiated when burst neurons activate motor neurons. Burst neurons are gated by pause neurons. The saccade generation network requires two conjoint inputs, one signalling the desired direction and amplitude of the movement and the other triggering when to initiate the movement. One main source of these signals is the superior colliculus which receives visual afferents from the retina as well as descending inputs from many cortical areas, in particular the lateral intraparietal area (LIP) in the posterior parietal cortex, frontal eye field (FEF) and supplementary eye field (SEF). FEF and SEF each project directly to the saccade generator. FEF and SEF may also regulate the activity of neurons in the superior colliculus through a basal ganglia circuit. The superior colliculus receives tonic inhibition from the substantia nigra pars reticulata. Neurons in the substantia nigra are themselves inhibited in relation to visually guided saccades by an oculomotor region of the caudate nucleus. The oculomotor region of the caudate nucleus is innervated by FEF and SEF. Visual signals reach LIP, FEF and SEF via a number of extrastriate visual areas (indicated by the multiple arrows) that are organized in a hierarchy originating in VI. V1 receives visual input from the dorsal lateral geniculate nucleus (LGNd) as well as the pulvinar which also projects to the various extrastriate visual areas including FEF. FEF and SEF receive input from other thalamic nuclei in and along the internal medullary lamina (IML) that are themselves innervated by afferents from the brainstem saccade generator, the superior colliculus and the substantia nigra.

Visually response neurons in the superficial layers of the superior colliculus have spatially restricted receptive fields and are arranged in a retinotopic map, but they respond equally for stimuli having different properties, such as color, orientation, or direction of motion /128/. In experiments using awake, behaving monkeys trained to fixate light spots for reward, the response of many of these cells is enhanced if the stimulus is used by the monkey as a target for a saccadic eye movement /60,181/. Further work has found this enhancement in a number of other visuomotor centers. The enhancement appears as either a larger initial response or an elevated activation after the initial visually evoked response. Furthermore, the enhanced activation can occur when a continuously visible stimulus is cued as the target for a saccade. This enhancement of the visual response of neurons in the superficial superior colliculus may signal the outcome of a selection process associated with the generation of a visually guided saccadic eye movement.

Neurons in the deeper layers of the superior colliculus discharge immediately before and during saccadic gaze changes /152/. At each location in the deeper layers of the superior colliculus neurons discharge in relation to saccades of a particular direction and amplitude. Thus, activation of cells in a particular location in the motor map will result in a saccade of a particular direction and amplitude. Through a process that is not completely understood, the spatial motor coordinates are converted into the temporal discharge patterns of burst cells /153/. The movement field of any single neuron and the areal extent of activation within the deep layers of the superior colliculus are quite large relative to the precision of saccadic eye movements. Therefore, the activation of many cells in one region of the motor map seems to be combined vectorially to produce a signal producing a single saccade /87,170/.

When multiple potential targets are available, a saccade resulting from the average of all the potential neuron contributions typically directs gaze to none of the targets. Humans and monkeys will actually produce saccades directing gaze to a point between two stimuli /51,115/ although this tendency is under voluntary control /66,95,116/. Saccade-related neurons in the superior colliculus discharge

before averaging saccades /57a,171a [added]/. The pattern of activation of the motor output neurons of the superior colliculus for averaging saccades produced in response to two simultaneously presented stimuli seems more or less the same as for normal saccades. This means that the specification of actual saccade direction and amplitude happens before the superior colliculus motor output neurons are fully activated. Hence, for an accurate saccade to just one among many stimuli the activation in the motor map of the superior colliculus must be limited to the cells responsible for generating just that saccade. But how does the brain insure that just one of the sites has become sufficiently more activated; in other words, when should a saccade be released?

Saccade initiation is prevented by inhibitory circuits at a number of levels; the brainstem pause neurons have already been described above. The movement cells in the motor map of the superior colliculus are tonically inhibited by fixation cells in the rostral end of the superior colliculus /107,108/ and by neurons in the substantia nigra pars reticulata /69/. It seems that a saccade will be initiated when these inhibitory circuits are shut off. If signals that represent the saccade vector needed to acquire a desired target location also suppress the inhibitory circuits, then a saccade of a particular direction and amplitude will be produced when one location in the motor map becomes sufficiently activated. If more than one location in the motor map becomes activated, then it will take further processing to resolve which of the potential sites of activation will become dominant and produce an eye movement. An accurate saccade will be produced only when one of the locations in the motor map becomes sufficiently active to release the inhibition. It is well known, however, that speed can prevail over accuracy in saccade production /116,173/. In the scheme I am sketching this could happen when the inhibition of saccade generation is released too early, either by an intrinsic threshold reduction or by an extrinsic trigger signal.

Most investigations of the superior colliculus have presented monkeys with a single stimulus as the target for an eye movement. However, Ottes and coworkers /117/ recorded from the superior colliculus in monkeys making saccades to one of two targets distinguished by color. Monkeys were

trained to generate a saccade to fixate a green target even when it was presented with a single red distractor. Neurons with visual or combined visual and saccade-related activity were analyzed. Ottes *et al.* reported no difference in the initial visual response to either the green target or the red distractor in the response field. Previous work had shown that neurons in the superior colliculus do not discriminate color /91/. The saccade-related activation of the cells occurred when a saccade was generated into the response field regardless of the stimulus configuration giving rise to that saccade, even if the movement was not rewarded. Upon closer examination of the data published by Ottes and coworkers, one can observe differential activation in the interval following the initial visual response but before the saccade. If the green target was in the response field, some cells discharged in a sustained fashion for 100-200 ms, leading up to the saccade-related burst. This prelude of activation was absent if the specified target was not in the response field. Thus, this prelude of activation may reflect the process of specifying which stimulus will become the target of the saccade. Further evidence has been obtained that the prelude of activity of saccade-related neurons in the superior colliculus reflects the response selection process /57/. Monkeys were trained to make a saccade to one of two stimuli specified by a color signal presented as a foveated stimulus. Once the fixated stimulus specified that the stimulus in a cell's response field was to be the target, the low-frequency prelude of activity commenced and continued until a subsequent signal triggered the saccade to the target. If the stimulus in the response field was not the target for the movement, a degree of activation was evident but at a lower level than if it was a target.

These data indicate that the movement cells in the superior colliculus reflect the outcome of the target selection process, but it is less clear how the neurons participate in the decision. The problem of saccade target selection amounts to insuring activation of the neurons in just the one appropriate location of the motor map in the superior colliculus. Initially there may be a low level of activation in the superior colliculus motor map related to many potential saccade targets. Activation must grow for locations corresponding to more likely or cons-

picuous targets, yielding a burst that triggers the saccade occurring at just one location in the motor map. The process by which activation in just one region is insured may depend on intrinsic inhibitory interactions /171/, but because superior colliculus neurons do not discriminate visual features afferents from the cerebral cortex must be used.

ROLE OF FRONTAL EYE FIELD IN SACCADE TARGET SELECTION

The frontal eye field (FEF) in the rostral bank of the arcuate sulcus (Figure 1), represents the final stage of cortical processing before a visually guided saccadic eye movement occurs /22,59,134/. At least two other areas in the cerebral cortex are directly involved in saccade production, the lateral intraparietal area (LIP) in the posterior parietal cortex /7,13,14/ and the supplementary eye field situated on the crown of the cortex dorsomedial to the FEF /90,133,145/. Unfortunately, at present there is no information about the role of these two areas in saccade target selection.

Different functional types of neurons have been identified in FEF. Among these, certain neurons are visually responsive; others discharge before and during saccadic eye movements, and others exhibit both visually-elicited and saccade-related activation. Each of these populations of neurons responds to stimuli in particular parts of the visual field or before saccades of particular directions and amplitudes. Intracortical electrical stimulation in FEF with currents of less than 50 μA elicits saccadic eye movements /25/. Mapping the representation of saccades in FEF with microstimulation has demonstrated that saccade amplitude is laid out in FEF with the shortest saccades represented ventrolaterally and longer saccades dorsomedially /25, 126/. This pattern of mapping is consistent with the finding that the receptive fields of visual cells in the lateral prearcuate cortex represent the central visual field, and dorsomedial cells the peripheral visual field /158/. The signal output by the FEF to the oculomotor system appears to be the retinotopic goal of the next saccade /43,146/.

FEF innervates other oculomotor structures. Neurons that discharge specifically before and

during saccades send axons to the superior colliculus /150/ and to the brainstem saccade generating circuit /149/. Each site in FEF excites the site in the superior colliculus representing the same saccade and inhibits surrounding sites in the superior colliculus /146/. The projection to the brainstem saccade-related structures has also been demonstrated in anatomical studies /71,148,155/. The FEF is connected to the superior colliculus in a topographic fashion /53,82,156/ as well as to other subcortical targets, such as the oculomotor zones of the caudate nucleus and the thalamus /71,118,156/.

FEF is also connected with a large number of visual cortical areas /72,88,154/. In our own work /99,136-139/ we have found that convergence from the dorsal and ventral processing streams occurs in lateral FEF but not in medial FEF (Figure 1). In particular, whereas the caudal inferior temporal cortex projects mainly to the lateral FEF, area LIP in the posterior parietal cortex projects throughout FEF. Also, the dorsal bank of the superior temporal sulcus projects to medial FEF; the ventral bank, to lateral FEF, and the fundus, throughout FEF. In addition, certain extrastriate areas with retinotopic visual field organizations, such as area MT, project topographically onto FEF. Thus, lateral FEF, which is responsible for generating short saccades, receives visual afferents from the foveal representation in retinotopically organized areas, from areas that represent central vision in the inferotemporal cortex and from other areas having no retinotopic order. In contrast, medial FEF, which is responsible for generating longer saccades, is innervated by the peripheral visual field representation of retinotopically organized areas, from areas that emphasize peripheral vision or are multimodal, and from other areas that have no retinotopic order.

Physiological recordings in the FEF of monkeys trained in visual tracking tasks have shown that roughly half of the cells respond to visual stimuli /24,58,83,97,121,132,157,180/. The latency of response is typically 60 to 100 msec. The receptive fields are large, emphasizing the contralateral hemifield but often extending into the ipsilateral. As previously observed in the superior colliculus, the response of the visual cells is enhanced if the stimulus is the target for a saccade /58,180/. This enhancement is not observed if the stimulus falls outside a neuron's receptive field or if the monkey is not required to make a saccade but responds otherwise to the stimulus. In all of these experiments, the monkey is generally presented with a single stimulus that is the target for the saccade. To investigate the process of target selection itself, a choice must be provided by presenting multiple stimuli, in essence creating a visual search task.

In visual search tasks a target stimulus is presented simultaneously with multiple distractor stimuli; the target may be distinguished from the distractors on the basis of a single feature, such as color or orientation, or on the basis of combinations of features known as conjunctions. An extensive literature has evolved exploring human visual search performance under a variety of conditions /165, 178/. Only a couple of basic findings need to be understood for our purposes. If the difference between the target and distractor features is large (e.g., a red target among green distractors), then the time to respond to the target is not influenced by the number of distractors. This performance has been referred to as "pop out" or "parallel" search because the target is effortlessly discriminated from any number of distractors. If the target is not easily discriminated because the difference between the features is small (e.g., a target line oriented at 80° among 90° distractors) or no single feature distinguishes the stimuli (e.g., "T" among "L"s), then the time to respond to the target increases as more distractors are added to the display. This performance has been referred to as "serial" search because each stimulus must be inspected in turn to identify the target accurately. Such inspection can be done without shifting gaze but through moving visual attention /78/. Knowledge such as this acquired about discrimination performance using different visual search displays can be used to design experiments aimed at investigating neural mechanisms of target selection.

We have been investigating target selection by training rhesus monkeys to perform not only the single target tracking task but also a simple, pop-out visual search task. Such tasks have been used previously with macaque monkeys to investigate visual abilities /141/. We recorded the activity of single neurons in FEF in monkeys performing these two tasks /135/. Neurons with combined visual- and

eye movement-related activity were analyzed because they were active during target identification and response selection. A representative neuron is illustrated in Figure 3. The initial responses of neurons to the search stimulus arrays did not differentiate whether the target or a distractor was in the response field. However, the activity of the neurons ultimately evolved to specify target location before the execution of the saccade. If the target was in the response field, then the activity peaked, but the activity was suppressed when the target was beside but not distant from the response field. This finding was quite common in the visuomovement neurons we studied. We have also analyzed the activity of neurons with exclusively visual responses /162/. The common finding was that visual cells in FEF did not discriminate the target from the distractor in any way. We have analyzed the level, time course and duration of activation of the cells when the target was presented alone or with distractors and have found no discernible differences in the neurons sampled to date. We are currently investigating how these findings relate to the aforementioned visual response enhancement. We have also analyzed a population of movement cells. These discharged in association with saccades into the movement field whether the target was presented alone or with distractors.

These preliminary findings have a number of implications. First, using search stimulus displays that are flashed on, FEF cells exhibit an initial, non-discriminating response. This finding is particularly interesting because, as described below, feature selective cells in primary visual cortex do respond differentially from the onset of their activation. This implies that FEF visual neurons receive convergent afferents from neurons representing many features at one retinotopic location. The anatomical data referred to above allow this possibility. Second, the activation of visuomovement neurons evolved before the saccade, becoming most active if the target was in the response field and becoming attenuated if the salient target was near its response field. Based on the spatial tuning of these neurons, it seems reasonable to suppose that this suppression reduces the probability of an eye movement to the distractor inside the response field. The observed facilitation surrounded by suppression of visuomovement
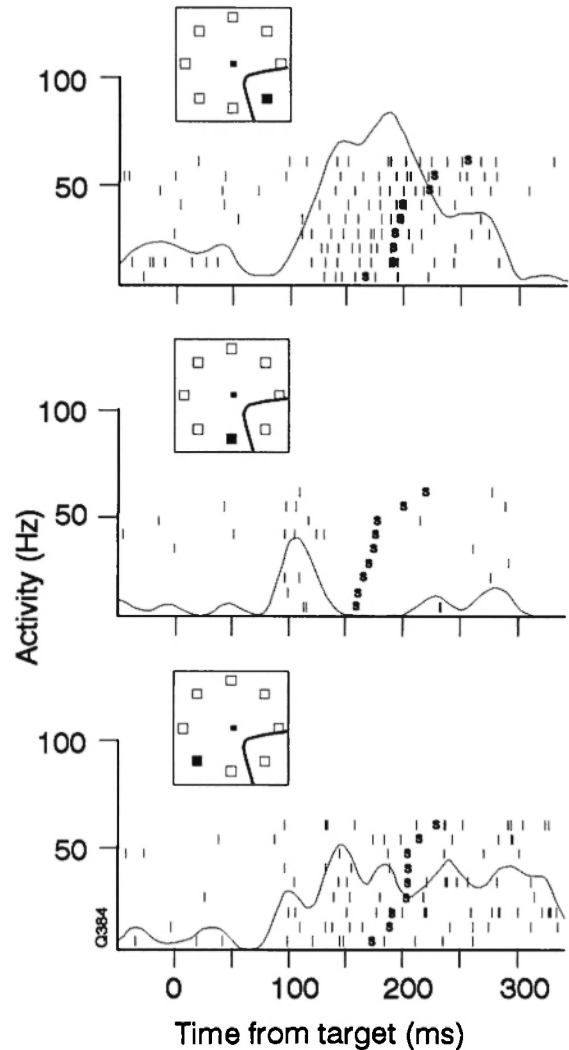

Fig. 3: Activation of a FEF visuomovement neuron during visual search. Each panel illustrates neural activation in two ways. First, each vertical tickmark indicates the time of an action potential in a raster display; each row is from a different trial. Also, the average density of spikes as a function of time is shown. The rasters and spike density function are aligned on the time of target presentation; the 's' symbol indicates the time of saccade initiation in each trial. When the target was in the response field (top panel), the activation was similar to that observed when the target was presented alone at the same location. When the target was distant from the response field (bottom panel), the neuron responded to the distractor in the response field and continued discharging at a reduced rate until the saccade. When the target fell beside the response field (middle panel), the neuron discharged only briefly, becoming inactive prior to the saccade.

neuron activity resembles the center-surround receptive field organization of neurons in the early visual system and may likewise arise through lateral inhibition. In summary, these results demonstrate one possible mechanism by which a desired target is fixated and inappropriate eye movements are prevented.

To the extent that saccades are normally produced in a very cluttered visual environment, studying saccade target selection with the visual search tasks just described will provide limited information. In this context, a recent study by Burman and Segraves is important because they investigated the activity of neurons in FEF of monkeys scanning complex natural images /26/. Burman and Segraves found that the activity of movement cells was the same for saccades produced in response to light spots as for saccades produced to scan a natural image. The activity of visually responsive cells during scanning behavior, however, varied according to whether the subsequent saccade was made to a feature in the cells' receptive field. On average visual cells were activated if the next saccade was to a feature in their receptive field, and were suppressed preceding saccades to features outside the cells' receptive field. This finding indicates that the visual cells in FEF usually signal whether the upcoming saccade will be into the cell's receptive field, although close examination of the data reveals that this relationship can be quite variable. For example, Figure 3C of Burman and Segraves /26/ shows a raster display of the activity of a visual cell before saccades made to parts of the image that were in the cell's receptive field. Sometimes the neuron was activated after a specific, short latency once gaze landed in the current fixation; this tended to occur near the bottom of the raster which represents later saccades in the scanning. Other times the same neuron was not activated or not modulated before the saccade; these tended to occur near the top of the raster which represents earlier saccades. This analysis indicates that the visual cell activity reliably predicted where the upcoming saccade would go following only certain fixations. When the visual response occurred with a consistent, short latency, it seems to indicate that the decision about the next saccade target was made either very rapidly

following or even before the fixation in question. But how could the decision be made at such a time? One possibility involves the observation described earlier that the pattern of eye movements made to inspect a complex image often exhibits a repetitive scanpath. Thus, perhaps in the early period of scanning the monkey had not established a scanpath, so the choice of saccade target was constantly evolving and being updated. In fact, in this early period, shown in the rasters at the top in Figure 3C of Burman and Segraves /26/, the activity of the visual neuron was less predictive of saccade target. However, as the scanpath became established, the target for each saccade following a given fixation became more regular and predictable. In this later period the visual neuron could discharge with a specific latency following fixation because target selection had already occurred. Interestingly, there appeared to be a corresponding change in fixation duration as scanning progressed during collection of the data from the cell in Figure 3; early on the fixation durations tended to be long and variable whereas later in the scanning the fixation durations became shorter and more regular. Curiously, this evolution of fixation durations is actually opposite to the general tendencies that have been observed for humans viewing pictures /8/. Burman and Segraves made the additional very interesting finding that when the monkey retraced the original scanpath over the image by following a spot of light, the visual cell responses were delayed until the presentation of the tracking spot, even though the visual image and subsequent saccade were identical to what had previously elicited activation earlier after fixation. This final finding shows that the visual responses of FEF neurons are sensitive to the context in which the target selection occurs.

In summary, these findings from our laboratory and from Burman and Segraves show quite clearly that FEF is active during the process of target selection during natural scanning eye movements. This preliminary work frames many questions for future research. Where and how are the visual responses of FEF neurons gated? Are intrinsic interactions responsible for the evolution of activity in visual and visuomovement cells? What do the visual afferents to FEF signal about target location? How is the processing in FEF linked to what is hap-

pening in other visuomotor centers, such as SEF and LIP as well as subcortical structures?

The interpretation of the role of FEF in saccade target selection must consider the effects of FEF lesions. In general, brain lesions involving FEF do not prevent the generation of visually guided saccades; the common effects involve impairments in generating voluntary saccades. For example, patients are unable to direct a saccade in the direction opposite to that of a flashed target /62/. Monkeys suffer a loss in predictive saccadic eye movements /23,75/ and an inability to generate saccades to remembered locations /43a/. In humans, following frontal cortex damage patients exhibit difficulties in instructed visual scanning /89/ and in visual search /33,74,161/. For example, one patient with right frontal lobe damage made no saccades into the left visual field during scanning of static visual scenes /101/. In monkeys, lesions of the FEF and surrounding cortex impair visual search when the task involves multiple eye movements to find a target /38,85/. The time to find a target embedded in distractors and the number of errors both increase following FEF lesions /86/; in particular, monkeys with lesioned FEF fail to exhibit inhibition of return in their search pattern, looking more often than normal to image locations they have already viewed. When monkeys are tested in a task comparable to that used in our recordings, requiring a single saccade to one odd target in an array, then FEF lesions do not increase the latencies of the saccades /142/; unfortunately, this study did not report the error rates, nor the time course of the effects.

The results of these ablation studies indicate that individuals can ultimately recover the ability to generate saccades following FEF lesions. Other experiments have demonstrated that the superior colliculus is primarily responsible for this ability. Combined, bilateral lesions of the FEF and superior colliculi result in a permanent loss of saccadic eye movements /144/. This work indicates that two parallel pathways are normally involved in the generation of saccades: the subcortical pathway depends on the superior colliculus, and the cortical pathway is headed by the FEF. A reasonable working hypothesis is that the subcortical pathway is responsible for reflexive, orienting saccades, and

the cortical pathway is responsible for the more voluntary, visually instructed saccades. This is borne out by the effect of FEF and superior colliculus lesions on saccade latency; ablation of the superior colliculus but not FEF results in a loss of the short latency, express saccades /142/. It appears, then, that the FEF functions in a more discriminating fashion than does the superior colliculus. This it can do by virtue of the constellation of afferents FEF receives from other cortical areas as described above. In fact, this anatomical organization provides a framework within which to interpret the functional contributions of other cortical visual areas toward saccade target selection.

ROLES OF VISUAL CORTEX IN TARGET SELECTION

Visual selection depends on the differential responses of neurons in the early visual system to stimuli having different feature attributes, such as orientation, direction of motion, color or spatial frequency. This idea is motivated by psychophysical as well as physiological studies. As mentioned above, work by a number of investigators has shown that discrimination of stimuli is easier if the stimuli differ along particular visual feature dimensions, e.g., different colors or orientations. The list of simple features that support effortless discrimination corresponds more or less to the types of features which single neurons in the visual cortex discriminate.

If feature selective neural responses are the basis of visual selection, then two questions arise. First, when do single neurons discriminate stimuli in the course of their activation? Second, how does the brain make use of such signals? We will consider these questions in turn. Recordings in primate V1 indicate that the stimulus preference of neurons is expressed virtually as soon as the cell can respond /31,80,163,175; but see 47/. In other words, if the stimulus is within the optimal range, then neurons fire, but if the stimulus is outside the optimal range, then the neurons have no period of even slight activation. This is illustrated in Figure 4. Similarly, the responses of V2 neurons to real and illusory contours are selective as soon as a response is possible /176/. Face-selective neurons in the inferior

temporal (IT) lobe also express their selectivity quite soon from the beginning of their response /114,164/ (Figure 4). For these IT cells the latency of response was 90 ms on average, and statistically reliable discrimination was achieved within another 20-30 ms and improved in reliability for another 60 ms. Although the cells remained active, the reliability of the discrimination decreased because of
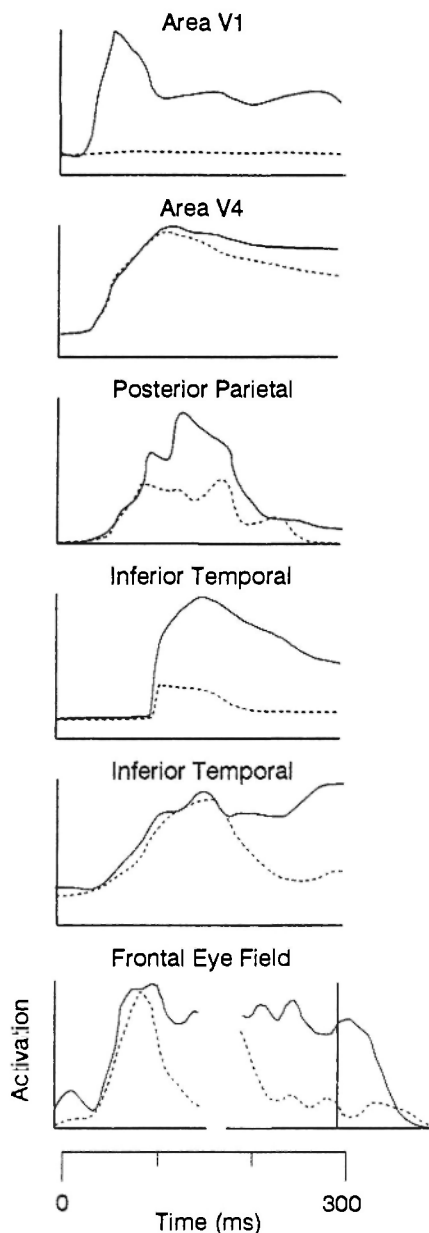
increased variability in the activity level. When masking stimuli are presented at different intervals after an optimum face stimulus, the neural activity is eliminated following a mask delay of 20 ms; this mask delay value corresponds to the perceptual threshold /130/. These results taken together indicate that when presented with a single stimulus, visual neurons signal according to their particular mode of selectivity as soon as they are active, and that a reliable discriminative signal is available in the first few action potentials issued by a neuron.

We turn now to the question of how selective neural responses are used to make perceptual decisions. Recent studies have used signal detection theory to compare the discrimination performance of neurons with psychophysical abilities /20,21,174/. It appears that signals generated by a small number

Fig. 4: Time course of selective activation of cortical neurons. Representative figures, redrawn from the cited publications, are illustrated with the same time scale and normalized amplitude for comparison. The top panel illustrates the response profiles for neurons in V1 in response to an optimally oriented stimulus (solid line) and an orthogonally oriented stimulus (dashed line) /31,92/. The second panel illustrates the response of neurons in V4 to a stimulus that matches (solid line) or does not match (dashed line) a cue stimulus /103/. The third panel shows the activity of a neuron in posterior parietal cortex to a pair of stimuli when the stimulus in the receptive field is the target for a saccade (solid line) and when the other stimulus is the target for a saccade (dashed line) /27/. The fourth panel shows the activation of neurons in inferior temporal cortex in response to an optimum face stimulus (solid line) and a non-optimum stimulus (dashed line) /114/. The fifth panel illustrates the activation of inferior temporal neurons to the same stimulus array when the optimal stimulus is specified as the target for a saccade (solid line) and when a non-optimal stimulus was specified as the target (dashed line) /34/. The bottom panel shows the evolution of activation of a visuomovement neuron in frontal eye field relative to stimulus presentation (left) and saccade initiation (right) when the target was in the receptive field (solid line) and when the target was beside the receptive field (dashed line) /135/.

of cells may be sufficient to discriminate stimuli reliably. It is important to note that the discrimination takes time. For example, estimates of the discrimination threshold of neurons in MT decrease as longer intervals of activation are measured; a corresponding change in perceptual discrimination was also observed /21/. In general, as longer durations of activation are measured, noisy variations in firing rate make less of a difference; this has been incorporated in one model of how the activity of feature-selective neurons can be used to discriminate stimuli in a visual search task /184/. One outcome of this model, based on physiological data from V1, is that a reliable perceptual discrimination may require something like at least 150 ms of activation. We should not forget that the temporal discharge pattern as well as the rate may contribute to neural decision making /10,55,94/. However, the extremely short intervals needed for discriminable activation of visual cortex neurons to evolve may limit the amount of time available for temporal patterns to be registered.

The foregoing discussion regards local decision processes about one stimulus within a neuron's receptive field. When more than one stimulus is in view, interactions occur between neurons responding to stimuli in neighboring parts of the scene which provide the basis visual selection by comparing features across the visual field. Such comparisons entail horizontal interactions between cells in topographic maps of visual areas. There is good evidence that the response of a neuron to a stimulus in its receptive field may be modulated by the presentation of other stimuli outside its receptive field /3,17,56,109/. For example, in a recent physiological investigation most cells recorded in V1 were suppressed by an oriented texture pattern surrounding the receptive field, but some cells were more active when the orientation of the surround texture was orthogonal to the orientation of the stimulus in the receptive field /80/. These effects of a surrounding pattern on V1 neuron activation were expressed around 20 ms after the initial activation which indicates that they are the outcome of local or feedback processes. Similar interactions have been observed in motion processing areas MT and MST /2,113,131/, and suppressive receptive field surrounds have also been

observed in V4 /44,45/. These interactions seem to reveal the mechanism for segmentation of the image into figure and ground and identifying the location of features that are conspicuously different from surrounding features.

NEURAL CORRELATES OF VISUAL ATTENTION

The suppressive interactions just described may subserve early, bottom-up stages of visual selection by identifying the salient stimuli in different regions. However, gaze does not always shift to the most conspicuous parts of a scene. Another control mechanism in primates provides voluntary control over the locus of the most elaborate visual processing in the visual field. The focus of visual attention can be directed away from the focus of gaze /49,67,73,122/. Such shifts of attention can precede and thus may guide eye movements; but the link between gaze shifts and attention shifts, while common, is not obligatory /42,79,124,125,151/. A number of neurophysiological studies have investigated the activation of neurons when monkeys produce a voluntary shift of visual attention /35,46/.

The first identified modulation of neural activity related to directed visual attention was found in the posterior parietal cortex /27,127/. Monkeys were trained to respond to visual stimuli either with saccadic eye movements or by releasing a bar or reaching toward the light without shifting gaze. Under these circumstances, neurons in the posterior parietal cortex exhibited enhanced visual responsiveness even if a saccade was not made. Some of these data are illustrated in Figure 4. This dissociation of the visual response enhancement from saccade execution distinguishes the parietal cortex from the superior colliculus or FEF. It will be important to investigate the activity of neurons in the posterior parietal cortex when monkeys must discriminate targets from among many distractors.

Area V4 on the prelunate gyrus has been the focus of a number of physiological studies investigating the neural basis of visual attention and selection. Moran and Desimone /98/ demonstrated that when two stimuli were presented within the receptive field of a V4 neuron, the response of the cell was modulated according to which stimulus the

monkey was instructed to use for a matching task; in other words, if the optimal stimulus was used, the response was robust, but if the other, non-optimal stimulus was used, then the response of the neuron to the same stimulus configuration was attenuated. However, if only one of the two stimuli was in a cell's receptive field, then the influence on response was not observed. Other studies have also observed modulation of V4 neuronal responses to stimuli presented under different circumstances, requiring different degrees of attention on the part of the monkey /52,63,64,105/. One condition in the study by Henny *et al.* /63/ involved presentation of four oriented gratings equidistant from the fixation spot with one grating oriented differently from the other three. Cells were recorded in V4 while monkeys made a single saccade to fixate the odd oriented grating. Only a small fraction of the units exhibited any differential response to the stimulus in its receptive field if it was the target for a saccade or a distractor, and the cell illustrated in the paper was activated 250 ms after stimulus presentation.

Motter /102/ has shown that the responsiveness of neurons in V4 to the optimal stimulus in the receptive field was modulated by prior cuing about whether the stimulus was to be used in a feature discrimination judgment. The modulation of responsiveness was greatest when multiple distractors were present. In a subsequent study Motter /103,104/ investigated the activation of V4 neurons using a task in which monkeys selected a subset of visual stimuli to be used in a subsequent feature discrimination judgment based on a foveal cue. He found that neurons in V4 responded differentially to stimuli in their receptive field depending on whether the receptive field stimulus was selected for use in the judgment because they matched the foveal cue stimulus. The initial visual response to the array of bars, having a latency of 50 ms, was the same whether or not the receptive field stimulus matched the cue; after 120-170 ms the differential activation became established and persisted until the end of the trial (illustrated in Figure 4). This selective activation did not depend on the feature specificity of neurons, did not require the continued presence of the foveal cue and changed if the cue color was switched. According to Motter, V4 neurons may be responsible for selecting

stimuli in the visual field according to the presence of specific features. This kind of signal is an essential element for target localization during visual search; recent work has shown that humans can use features such as color or form to guide the allocation of visual attention /39,77/.

A recent study by Chelazzi and coworkers /34/ has provided information on the role of the inferior temporal cortex in selecting the target for a saccade. The activity of neurons was examined in the anterior inferior temporal cortex of monkeys making a saccade to the location of one stimulus in an array of stimuli that matched the appearance of a remembered cue stimulus. One of the stimuli used was optimum for each cell, and the other elicited little response. After the cue was presented, neurons discharged at a low rate throughout the 1500 ms delay period; this activation was somewhat higher if the cue was an optimal stimulus. When the choice stimulus array was presented with more than one stimulus in the large receptive field, the inferior temporal cells exhibited a 150 ms period of activation that did not vary with array configuration. However, 150-200 ms after choice array presentation, which was 90-120 ms before the saccade, the activation of the neurons changed to reflect target identity (Figure 4). That is, if the optimum stimulus was the target, then neuron activation remained elevated, discharging more once the saccade brought the optimal stimulus into the fovea. However, if the non-optimal stimulus was the target, then neuron activation was attenuated and remained so after fixation of the non-optimal stimulus. This finding indicates that signals of visual object identity can be modulated with localization signals for the guidance of eye movements. Anatomical evidence indicates that the region of anterior IT cortex in which this finding was made does not project directly to FEF but instead to the ventrolateral prefrontal cortex /11,138,166/ that then projects to FEF /154/. FEF gets input from more caudal parts of IT cortex /11,99,138/. The properties of visual cells in IT cortex vary from caudal to rostral. Neurons in the caudal inferotemporal cortex are selective for primary stimulus features, such as color orientation, and neurons selective for more elaborate shapes or faces are found in the rostral inferotemporal cortex /160/.

This routing of feature but not complex object information to FEF may be related to the common finding that eye movements are directed to features of objects, such as the eyes, nose and mouth of a face /76,182/.

The extrastriate visual cortical areas just described are linked by connections with the pulvinar nucleus of the thalamus. The results of a variety of studies of pulvinar function in primates have been summarized by surmising that the pulvinar participates in identifying salient stimuli /129/. The pulvinar has been subdivided into a collection of four nuclei, medial, lateral, inferior and anterior, that are distinguished on the basis of their connectivity and functional properties /32,128/. The inferior pulvinar receives input from the retina as well as from the ipsilateral superior colliculus. The inferior division of the pulvinar is reciprocally connected with VI and extrastriate visual areas. The lateral nucleus of the pulvinar receives input from the superior colliculus and pretectum and is interconnected primarily with extrastriate visual areas. While the inferior and lateral pulvinar nuclei are intimate with the visual pathways, the medial nucleus of the pulvinar forms different associations, being interconnected with the superior temporal gyrus, the inferior parietal lobule and the cingulate cortex, as well as the prefrontal cortex including FEF.

The response properties of neurons vary in the different subdivisions /128/. Most cells in the inferior and lateral subdivisions of the pulvinar are visually responsive with retinotopic receptive fields. However, in a dorsomedial portion of the lateral pulvinar visual responsiveness is less prominent and no retinotopy is evident. Neurons in inferior and lateral pulvinar exhibit some feature specificity. Many cells respond more vigorously when a visual stimulus is the target for a saccade. However, unlike their counterparts in the superior colliculus or FEF, neurons in the inferior and lateral segments of the pulvinar, whose responses are enhanced if a saccade is executed to the stimulus in their receptive field, exhibit enhancement even for stimuli outside their receptive field. In contrast, neurons in the dorsomedial sector of the lateral division show spatially selective enhanced responses to visual stimuli to which the monkey either shifts gaze or attends without shifting gaze /119/.

Using pharmacological manipulations, information has been acquired about the role of the dorsomedial sector of the lateral pulvinar in selective visual attention. In one experiment a GABA-agonist or antagonist was injected into the dorsomedial sector of monkeys performing a task requiring shifts of visual attention /120/. Monkeys were trained to respond to the appearance of a visual stimulus that appeared on either the left or right of the fixation point. The location of the stimulus could be cued by a prior stimulus. This task has been designed to investigate spatial shifts of visual attention in humans /122/. If the target appears at the cued location, the reaction time is faster than if the target appears elsewhere. This difference is believed to reflect the shift of a visual attention process anticipating the appearance of the target at the cued location. Increasing GABAergic inhibition in the dorsomedial lateral pulvinar with the agonist, muscimol, increased the reaction times, which suggests a slowing or other impairment of the shift of attention. In contrast, decreasing GABAergic inhibition with the antagonist bicuculline, facilitates the shift of attention in this task, as reflected in a reduction in reaction times. This finding seems to show that the dorsomedial sector of the lateral pulvinar is involved in the movement or reallocation of visual attention across the visual field.

The same pharmacological manipulation was performed in another experiment in which monkeys were required to discriminate the color of a stimulus presented at a previously cued location /46/. Inactivation of the retinotopic part of the lateral pulvinar impaired identification of the target color in the affected hemifield when a distractor was present in the unaffected hemifield but not when the target was presented alone or when the distractor was in the same hemifield as the target. These results indicate that the lateral pulvinar plays a role in filtering the visual image, preventing non-selected stimuli from influencing behavior.

Sensory systems are commonly considered as limited in capacity, able to process only some of the stimuli being transduced from the environment

/178/. But this notion can be questioned on a number of grounds /168/. For example, the notion of limited capacity in visual processing seems hard to reconcile with all the evidence for multiple, parallel visual representations throughout the brain. Having the neural circuits necessary to analyze each point in the visual field duplicated in hypercolumn after hypercolumn across the cortex, it is hard to see where any limitation on visual processing *per se* would arise. On the other side of the system, however, the production of movements has obvious functional limits. Thus, because only one saccade can be made at a time, the visual image must be analyzed such that one point becomes the target for the next saccade.

RESPONSE SELECTION

Understanding how perceptual decisions are made seems to require knowing how response selection works. How and when does sensory information influence motor preparation and execution? In considering the general problem of stimulus and response selection, distinctions are often made between processes subserving stimulus processing and selection, processes responsible for allocating attention and processes subserving motor response selection. In other words, is the activation of a neuron following presentation of a stimulus in one part of the visual field due to a visually elicited response, or because visual attention is directed to that location, or because a movement is going to be produced toward the stimulus? In fact, such distinctions may not be very useful in understanding sensorimotor integration. Nevertheless, to investigate the stimulus, attention or mnemonic and motor elements of processing, one must experimentally dissociate the processes.

Boussaoud and Wise /19/ designed a task for macaque monkeys in which the same stimulus, presented more than once, had different meanings for the monkey because of the reward contingencies. The same stimulus could guide a covert shift of attention or it could instruct a movement direction. Neurons in the frontal cortex tended to respond differently to the same stimulus when it guided an attention shift versus when it

instructed a movement direction. Among other findings, these investigators reported that neurons in the postarcuate premotor cortex /177/ responded more to the stimulus when it signaled movement direction, and cells in the prefrontal cortex responded more when the same stimulus cued the upcoming location of the movement stimulus. These results indicate differential roles for these cortical areas and that the same stimulus can elicit activity in different neurons at different times according to its meaning in the context of the desired behavior.

Another way to dissociate sensory or attentional activation from motor planning-related activation is to manipulate stimulus-response compatibility. Almost always eye or limb movements are directed toward the location of stimuli in the world; the direction of the stimulus and of the evoked movement are compatible. It is possible, however, for primates to generate arbitrary movements in a direction different from that of a stimulus. For example, humans and monkeys can be instructed to generate an anti-saccade in the direction opposite a visual stimulus /65/. In conditions that require movements that are incompatible with stimulus locations, neurons in the prefrontal cortex tend to discharge more in relation to the location of the stimulus /48,54/. However, in cortical areas linked to movement production, cells are more commonly found that are active in relation to the movement direction as opposed to the stimulus direction /1,48,147/. It is important to note that these distinctions represent trends across populations of neurons with clear counter-examples in each area.

These results are important because they indicate the value of a strategy for elucidating the neural processing underlying target selection and saccade production. They also emphasize something Lashley /84/ said many years ago. The brain is never really dormant, even in an experimental animal. Responses to stimuli depend on the context in which the stimuli are presented.

SUMMARY

Saccade target selection must be understood in relation to the obvious fact that vision naturally occurs in a continuous cycle of fixations interrupted

by gaze shifts. The guidance of eye movements requires information about what is where in the visual field. The identities of objects are derived from their visible features. Single neurons in the visual system represent the presence of specific features by the level of activation; the reliability of the discriminating signal from single neurons varies over time. Each point in the visual field is represented by many populations of neurons activated by all types of features. Topographic representations are found throughout the visual and oculomotor systems; neighboring neurons tend to represent similar visual field locations or saccades. Selecting one out of many stimuli to which to direct gaze requires comparing stimulus attributes across the visual field. The existence of retinotopic maps of the visual field makes possible local interactions to implement such comparisons /41/. For example, a lateral inhibition network can extract the location of the most conspicuous stimulus in the visual field /30,40,81/. Coordinated with this parallel visual processing is activation in structures responsible for producing the movement such as FEF and the superior colliculus. A saccade is produced when the neurons at one location within the motor maps become sufficiently active. One job of visual processing, then, is to ensure that only one site within a movement map becomes activated. This is done when the neurons signalling the location of the desired target develop enhanced activation while the neurons responding to other locations are attenuated. Saccade target selection often converts an initially ambiguous pattern of neural activation into a pattern that reliably signals one target location. The ambiguity may be reduced through prior knowledge of the likely target location or identity, and extraretinal signals reflecting such expectations can modulate the responsiveness of afferent visual neurons. Specifying the metrics of a saccade and triggering the movement are coordinated but dissociable processes. Speed-accuracy trade-offs can thereby be produced allowing the visuomotor system to produce a saccade that is inaccurate because it is premature relative to the target selection process.

While there are many gaps in our knowledge, the questions to ask seem reasonably clear. Because saccade target selection involves visual processing

and eye movement programming combined with mnemonic influences, only continued experimental ingenuity will disentangle the various and variable contributions of individual neurons. With more experimental work we can anticipate a significant improvement in our understanding of how the brain selects the targets for saccades, so this should be a very active area of research in coming years.

REFERENCES

1. Alexander GE, Crutcher MD. Neural representations of the target (goal) of visually guided arm movements in three motor areas of the monkey. J Neurophysiol 1990; 64: 164-178.

2. Allman JM, Miezin F, McGuinness E. Direction and velocity specific surround in three cortical visual areas of the owl monkey. Perception 1985; 14: 105-126.

3. Allman JM, Miezin F, McGuinness E. Stimulus specific responses from beyond the classical receptive field: Neurophysiological mechanisms for local-global comparisons of visual motion. Ann Rev Neurosci 1985; 3: 532-548.

4. Allport A. Selection for action: Some behavioral and neurophysiological considerations of attention and action. In: Heuer H, Sanders AF, eds. Perspectives on Perception and Action. Hillsdale, NJ: Lawrence Erlbaum Associates, 1987: 395-419.

5. Aloimonos Y, Rosenfeld A. Computer vision. Science 1991; 253: 1249-1254.

6. Andersen RA, Asanuma C, Essick G, Siegel RM. Corticocortical connections of anatomically and physiologically defined subdivisions within the inferior parietal lobule. J Comp Neurol 1990; 296: 65-113.

7. Andersen RA, Bracewell M, Barash S, Gnadt J, Fogassi L. Eye position effects on visual, memory and saccade-related activity in areas LIP and 7a of macaque. J Neurosci 1990; 10: 1176-1196.

8. Antes JR. The time course of picture viewing. J Exp Psychol 1974; 103: 62-70.

9.   Bahill AT, Adler D, Stark L. Most naturally occur-
      ring saccades have magnitudes of 15 degrees or less.
      Invest Ophthalmol 1975; 14: 468-469.

10.   Bair W, Koch C, Newsome W, Britten K. Power
      spectrum analysis of bursting cells in area MT in the
      behaving monkey. J Neurosci 1994; 14: 2870-2892.

11.   Baizer JS, Ungerleider LG, Desimone R. Organiza-
      tion of visual inputs to the inferior temporal and
      posterior parietal cortex in macaques. J Neurosci
      1991; 11: 168-190.

12.   Ballard DH, Brown CM. Principles of animate
      vision. In: Aloimonos Y, ed. Active Perception.
      Hillsdale, NJ: Lawrence Erlbaum Associates, 1993:
      245-282.

13.   Barash S, Bracewell RM, Fogassi L, Gnadt JW,
      Andersen RA. Saccade-related activity in the lateral
      intraparietal area. I. Temporal properties:
      Comparison with area 7a. J Neurophysiol 1991; 66:
      1095-1108.

14.   Barash S, Bracewell RM, Fogassi L, Gnadt JW,
      Andersen RA. Saccade-related activity in the lateral
      intraparietal area. II. Spatial properties. J
      Neurophysiol 1991; 66: 1109-1124.

15.   Biederman I, Rabinowitz JC, Glass AL, Stacy EW.
      On the information extracted from a glance at a
      scene. J Exp Psychol 1974; 103: 597-600.

16.   Biguer B, Prablanc C, Jeannerod M. The contribu-
      tion of coordinated eye and head movements in hand
      pointing accuracy. Exp Brain Res 1984; 55: 462-
      469.

17.   Blakemore C, Tobin EA. Lateral inhibition between
      orientation detectors in the cat's visual cortex. Exp
      Brain Res 1972; 15: 439-440.

18.   Boussaoud D, Ungerleider LG, Desimone R.
      Pathways for motion analysis: Cortical connections
      of the medial superior temporal and fundus of the
      superior temporal visual areas in the macaque. J
      Comp Neurol 1990; 296: 462-495.

19.   Boussaoud D, Wise SP. Primate frontal cortex:
      neuronal activity following attentional versus
      intentional cues. Exp Brain Res 1993; 95: 15-27.

20.   Bradley A, Skottun BC, Ohzawa I, Sclar G, Freeman
      RD. Visual orientation and spatial frequency dis-
      crimination. A comparison of single neurons and
      behavior. J Neurophysiol 1987; 57: 755-772.

21.   Britten KH, Shadlen MN, Newsome WT, Movshon
      JA. The analysis of visual motion: A comparison of
      neuronal and psychophysical performance. J
      Neurosci 1992; 12: 4745-4765.

22.   Bruce CJ. Integration of sensory and motor signals
      for saccadic eye movements in the primate frontal
      eye fields. In: Edelman GM, Gall WE, Cowan WM,
      eds. Signals and Sense, Local and Global Order in
      Perceptual Maps. New York: John Wiley and Sons,
      1990: 261-314.

23.   Bruce CJ, Borden JA. The primate frontal eye fields

24.   are necessary for predictive saccadic tracking. Soc
      Neurosci Abstr 1986; 12: 1086.

24.   Bruce CJ, Goldberg ME. Primate frontal eye fields.
      I. Single neurons discharging before saccades. J
      Neurophysiol 1985; 53: 603-635.

25.   Bruce CJ, Goldberg ME, Bushnell C, Stanton GB.
      Primate frontal eye fields. II. Physiological and
      anatomical correlates of electrically evoked eye
      movements. J Neurophysiol 1985; 54: 714-734.

26.   Burman DD, Segraves MA. Primate frontal eye field
      activity during natural scanning eye movements. J
      Neurophysiol 1994; 71: 1266-1271.

27.   Bushnell MC, Goldberg ME, Robinson DL.
      Behavioral enhancement of visual responses in
      monkey cerebral cortex. I. Modulation in posterior
      parietal cortex related to selective visual attention. J
      Neurophysiol 1981; 46: 755-772.

28.   Carpenter RHS, ed. Eye Movements. Vol. 8 in:
      Cronly-Dillon J, ed. Vision and Visual Dysfunction,
      London: Macmillan, 1991.

29.   Carpenter RHS. The visual origins of ocular motility.
      In: Carpenter RHS, ed. Eye Movements, vol. 8 in:
      Cronly-Dillon J, ed. Vision and Visual dysfunction,
      London: Macmillan, 1991; 1-10.

30.   Cave KR, Wolfe JM. Modeling the role of parallel
      processing in visual search. Cognitive Psychology
      1990; 22: 225-271.

31.   Celebrini S, thorpe S, Trotter Y, Imbert M.
      Dynamics of orientation coding in area VI of the
      awake primate. Visual Neurosci 1993; 10: 811-825.

32.   Chalupa LM. Visual function of the pulvinar. In:
      Leventhal AG, ed. Vision and Visual Dysfunction
      Volume 4: The Neural Basis of Visual Function.
      London: Macmillan Press, 1991: 140-159.

33.   Chedru F, Leblanc M, Lhermitte F. Visual searching
      in normal and brain-damaged subjects (contribution
      to the study of unilateral inattention). Cortex 1973;
      9: 94-111.

34.   Chelazzi L, Miller EK, Duncaan J, Desimone R. A
      neural basis for visual search in inferior temporal
      cortex. Nature 1993; 363: 345-347.

35.   Colby CL. The neuroanatomy and neurophysiology
      of attention. J Child Neurol 1991; 6: S90-S118.

36.   Colby CL, Duhamel J-R. Heterogeneity of
      extrastriate visual areas and multiple parietal areas
      in the macaque monkey. Neuropsychologia 1991; 29:
      517-537.

37.   Colby CL, Gattass R, Olson CR, Gross CG. Topo-
      graphical organization of cortical afferents to
      extrastriate visual area PO in the macaque: A dual
      tracer study. J Comp Neurol 1988; 269: 392-413.

38.   Collin NG, Cowey A, Latto R, Marzi C. The role of
      frontal eye-fields and superior colliculi in visual
      search and non-visual search in rhesus monkeys.
      Behav Brain Res 1982; 4: 177-193.

39.   Corbetta M, Miezin FM, Dobmeyer S, Shulman GL,

Petersen SE. Selected and divided attention during visual discriminations of shape, color and speed: Functional anatomy by positron emission topography. J Neurosci 1991; 11: 2383-2402.

40. Cornsweet TN. Visual Perception. New York: Academic Press, 1970.

41. Cowey A. Why are there so many visual areas? In: Schmitt FO, Worden FG, Adelman G, Dennis SG, eds. The Organization of the Cerebral Cortex. Cambridge MA: MIT Press, 1981: 395-413.

42. Crawford TJ, Muller HJ. Spatial and temporal effects of spatial attention on human saccadic eye movements. Vision Res 1992; 32: 293-304.

43. Dassonville P, Schlag J, Schlag-Rey M. The frontal eye field provides the goal of saccadic eye movement. Exp Brain Res 1992; 89: 300-310.

43a. Deng S-Y, Goldberg ME, Segraves MA, Ungerleider LG, Mishkin M. The effect of unilateral ablation of the frontal eye fields on saccadic performance in the monkey. In: Keller El, Zee DS, eds, Adaptive Processes in Visual and Oculomotor systems. Oxford: Pergamon, 1986: 201-208.

44. Desimone R, Schein SJ. Visual properties of neurons in area V4 of the macaque: Sensitivity to stimulus form. J Neurophysiol 1987; 57: 835-868.

45. Desimone R, Schein SJ, Moran J, Ungerleider LG. Contour, color and shape analysis beyond the striate cortex. Vision Res 1985; 25: 441-452.

46. Desimone R, Wessinger M, Thomas L, Schneider W. Attentional control of visual perception: Cortical and subcortical mechanisms. Cold Spring Harbor Symp Quant Biol 1990; 55: 963-971.

47. Dinse HR, Krüger K, Best J. A temporal structure of cortical information processing. Concepts in Neuroscience 1990; 1: 199-238.

48. di Pellegrino G, Wise SP. Visuospatial versus visuomotor activity in the premotor and prefrontal cortex of a primate. J Neurosci 1993; 13: 1227-1243.

49. Eriksen CW, Hoffman JE. Temporal and spatial characteristics of selective encoding from visual displays. Percept Psychophys 1972; 12: 201-204.

50. Felleman DJ, Van Essen DC. Distributed hierarchical processing in the primate cerebral cortex. Cerebral Cortex 1991; 1: 1-47.

51. Findlay JM. Global visual processing for saccadic eye movements. Vision Res 1982; 22: 1033-1045.

52. Fischer B, Boch R. Peripheral attention versus central fixation: Modulation of the visual activity of prelunate cortical cells of the rhesus monkey. Exp Brain Res 1985; 345: 111-123.

53. Fries W. Cortical projections to the superior colliculus in the macaque monkey: A retrograde study using horseradish peroxidase. J Comp Neurol 1984; 230: 55-76.

54. Funahashi S, Chafee MV, Goldman-Rakic PS. Prefrontal neuronal activity in rhesus monkeys performing a delayed anti-saccade task. Nature 1993; 365: 753-756.

55. Geisler WS, Albrecht DG, Salvi RJ, Saunders SS. Discrimination performance of single neurons: Rate and temporal-pattern information. J Neurophysiol 1991; 66: 334-362.

56. Gilbert CD. Horizontal integration and cortical dynamics. Neuron 1992; 9: 1-13.

57. Glimcher PW, Sparks DL. Movement selection in advance of action in superior colliculus. Nature 1992; 355: 542-545.

57a. Glimcher PW, Sparks DL. Representation of averaging saccades in the superior colliculus of the monkey. Exp Brain Res 1993; 95: 429-435.

58. Goldberg ME, Bushnell MC. Behavioral enhancement of visual responses in monkey cerebral cortex. II. Modulation in frontal eye fields specifically related to saccades. J Neurophysiol 1981; 46: 773-787.

59. Goldberg ME, Segraves MA. Visual and frontal cortices. In: Wurtz RH, Goldberg ME, eds. The Neurobiology of Saccadic Eye Movements. New York: Elsevier, 1989: 283-313.

60. Goldberg ME, Wurtz RH. Activity of superior colliculus in behaving monkey. II. Effect of attention on neuronal responses. J Neurophysiol 1972; 35: 560-574.

61. Goodale MA, Milner AD. Separate visual pathways for perception and action. TINS 1992; 15: 20-25.

62. Guitton D, Buchtel HA, Douglas RM. Frontal lobe lesions in man cause difficulties in suppressing reflexive glances and in generating goal-directed saccades. Exp Brain Res 1985; 58: 455-472.

63. Haenny PE, Maunsell JHR, Schiller PH. State dependent activity in monkey visual cortex. II. Retinal and extraretinal factors in V4. Exp Brain Res 1988.

64. Haenny PE, Schiller PH. State dependent activity in monkey visual cortex. I. Single cell activity in V1 and V4 on visual tasks. Exp Braian Res 1988; 69: 225-244.

65. Hallett PE, Adams BD. The predictability of saccadic latency in a novel voluntary oculomotor task. Vision Res 1980; 20: 329-339.

66. He PY, Kowler E. The role of location probability in the programming of saccades: Implications for 'center-of-gravity' tendencies. Vision Res 1989; 29: 1165-1181.

67. Helmholtz H. Treatise on Psychological Optics. New York: Dover, 1865/1962.

68. Heywood CA, Cowey A. On the role of cortical area V4 in the discrimination of hue and pattern in macaque monkeys. J Neurosci 1987; 7: 2601-2617.

69. Hikosaka O, Wurtz RH. Visual and oculomotor functions of monkey substantia nigra pars reticulata. III. Memory-contingent visual and saccade responses. J Neurophysiol 1983; 49: 1268-1284.

70. Hubel DH, Wiesel TN. Receptive fields and functional architecture of monkey striate cortex. J Physiol (Lond) 1968; 195: 215-243.

71. Huerta MF, Krubitzer LA, Kaas JH. Frontal eye field as defined by intracortical microstimulation in squirrel monkeys, owl monkeys and macaque monkeys. I. Subcortical connections. J Comp Neurol 1986; 253: 415-439.

72. Huerta MF, Krubitzer LA, Kaas JH. Frontal eye field as defined by intracortical microstimulation in squirrel monkeys, owl monkeys and macaque monkeys. II. Cortical connections. J Comp Neurol 1987; 265: 332-361.

73. Jonides J. Towards a model of the mind's eye's movement. Can J Psychol 1980; 34: 103-112.

74. Karpov BA, Luria AR, Yarbus AL. Disturbance of the structure of active perception in lesions of the posterior and anterior regions of the brain. Neuropsychologia 1968; 6: 157-166.

75. Keating EG. Frontal eye field lesions impair predictive and visually-guided pursuit eye movements. Exp Brain Res 1991; 86: 311-323.

76. Keating CF, Keating EG. Monkeys and mug shots: Cues used by rhesus monkeys (Macaca mulatta) to recognize a human face. J Comp Psychol 1993; 107: 131-139.

77. Kim M-S, Cave KR. Spatial attention in searching for features and feature conjunctions. Poster presented at Psychonomic Society Meeting, Washington, D.C., 1993.

78. Klein R, Farrell M. Search performance without eye movements. Percept Psychophys 1989; 46: 476-482.

79. Klein R, Kingstone A, Pontefract A. Orienting of visual attention. In: Rayner K, ed, Eye Movements and Visual Cognition: Scene Perception and Reading. New York: Springer-Verlag, 1992: 46-65.

80. Knierim JJ, Van Essen DC. Neuronal responses to static texture patterns in area V1 of the alert macaque monkey. J Neurophysiol 1992; 67: 961-980.

81. Koch C, Ullman S. Shifts in selective visual attention: towards the underlying neural circuitry. Human Neurobiology 1985; 4: 219-227.

82. Komatsu H, Suzuki H. Projections from the functional subdivisions of the frontal eye field to the superior colliculus in the monkey. Brain Res 1985; 327: 324-327.

83. Kubota K, Tonoike M, Mikami A. Neuronal activity in the monkey dorsolateral prefrontal cortex during a discrimination task with delay. Brain Res 1980; 183: 29-42.

84. Lashley KS. The prorblem of serial order in behavior. In: Jeffress LA, ed, Cerebral Mechanisms in Behavior: The Hixon Symposium. New York: Wiley, 1951: 112-146.

85. Latto R. The effects of bilateral frontal eye-field lesions on the learnring of visual search task by rhesus monkeys. Brain Res 1978; 147: 370-376.

86. Latto R. The effects of bilateral frontal eye-field, posterior parietal or superior collicular lesions on visual search in the rhesus monkey. Brain Res 1978; 146: 35-50.

87. Lee C, Rohrer WH, Sparks DL. Population coding of saccadiceye movements by neurons in the superior colliculus. Nature 1988; 332: 357-360.

88. Leichnetz GR, Goldberg ME. Higher centers concerned with eye movement and visual attention: Cerebral cortex and thalamus. In: Büttner-Evvever JA, ed, Neuroanatomy of the Oculomotor System. New York: Elsevier, 1988: 365-429.

89. Luria AR, Karpov BA, Yarbus AL. Disturbances of active visual perception with lesions of frontal lobes. Cortex 1966; 2: 202-212.

90. Mann SE, Thau R, Schiller PH. conditional task-related responses in monkey dorsomedial frontal cortex. Exp Brain Res 1988; 69: 460-468.

91. Marrocco RT, Li RH. Monkey superior colliculus: Properties of single cells and their afferent inputs. J Neurophysiol 1977; 40: 844-860.

92. Maunsell JHR, Gibson JR. Visual response latencies in striate cortex of the macaque monkey. J Neurophysiol 1992; 68: 1332-1344.

93. Maunsell JHR, Newsome WT. Visuala processing in monkey extrastriate cortex. Ann Rev Neurosci 1987; 10: 363-401.

94. McClurkin JW, Optican LM, Richmond BJ, Gawne TJ. Concurrent processing and complexity of temporally encoded neuronal messages in visual perception. Science 1991; 253: 675-677.

95. Menz C, Groner R. Saccadic programming with multiple targets under different task conditions. In: O'Regaana JK, Levy-Schoen A, eds, Eye Movements: From Physiology to Cognition. New York: Elsevier, 1987: 95-103.

96. Merigan WH, Maunsell JHR. How parallel are the primate visual pathways? Ann Rev Neurosci 1993; 16: 369-402.

97. Mohler CW, Goldberg ME, Wurtz RH. Visual receptive fields of frontal eye field neurons. Brain Res 1973; 61: 385-389.

98. Moran J, Desimone R. Selective attention gates visual processing in the extrastriate cortex. Science 1985; 229: 782-784.

99. Morel A, Bullier J. Cortical connections of intraparietal and inferotemporal visual areas in the macaque monkey: A double-labeling study. Soc Neurosci Abstr 1987; 177: 14.

100. Morel A, Bullier J. Anatomical segregation of two cortical visual pathways in the macaque monkey. Visual Neurosci 1990; 4: 555-578.

101. Moser A, Kömpf D. Unilateral visual exploration deficit in a frontal lobe lesion. Neuroophthalmol 1990; 10: 390-44.

102. Motter BC. Focal attention produces spatially selective processing in visual cortical areas VI, V2 and V4 in the presence of competing stimuli. J Neurophysiol 1993; 70: 909-919.

103. Motter BC. Neural correlates of attentive selection for color or luminance in extrastriate area V4. J Neurosci 1994; 14: 2178-2189.

104. Motter BC. Neural correlates of feature selective memory and pop-out in extrastriate area V4. J Neurosci 1994; 14: 2190-2199.

105. Mountcastle VB, Motter BC, Steinmetz MA, Sestokas AK. Common and differential effects of attentive fixation on the excitability of parietal and prestriate (V4) cortical visual neurons in the macaque monkeys. J Neurosci 1987; 7: 2239-2255.

106. Munk MHJ, Nowak LG, Bullier J. Spatio-temporal response properties and interactions of neurons in areas VI and V2 of the monkey. Soc Neurosci Abstr 1993; 19: 424.

107. Munoz DP, Wurtz RH. Fixation cells in monkey superior colliculus. I. Characteristics of cell discharge. J Neurophysiol 1993; 70: 559-575.

108. Munoz DP, Wurtz RH. Fixation cells in monkey superior colliculus. II. Reversible activation and de-activation. J Neurophysiol 1993; 70: 576-589.

109. Nelson JI, Frost BJ. Orientation-selective inhibition from beyond the classic visual receptive field. Brain Res 1978; 139: 359-365.

110. Neumann O. Visual attention and action. In: Neumann O, Prinz W, eds, Relationships between Perception and Action. Berlin: Springer-Verlag, 1990: 227-67.

111. Newsome WT, Pare EB. A selective impairment of motion perception following lesions of the middle temporal visual area (MT). J Neurosci 1988; 8: 2201-2211.

112. Noton D, Stark L. Scanpaths in saccadic eye movements while viewing and recognizing patterns. Vision Res 1971; 11: 929-942.

113. Olavarria JF, DeYoe EA, Knierim JJ, Fox JM, Van Essen DC. Neural responses to visual texture patterns in middle temporal area of the macaque monkey. J Neurorphysiol 1992; 68: 164-181.

114. Oram MW, Perrett DI. Time course of neural responses discriminating different views of the face and head. J Neurophysiol 1992; 68: 70-84.

115. Ottes FP, Van Gisbergen JAM, Eggermont JJ. Metrics of saccade responses to visual double stimuli: Two different modes. Vision Res 1984; 24: 1169-1179.

116. Ottes FP, Van Gisbergen JAM, Eggermont JJ. Latency dependence of colour-based target vs nontarget discrimination by the saccadic system. Vision Res 1985; 25: 849-862.

117. Ottes FP, Van Gisbergen JAM, Eggermont JJ. collicular involvement in a saccadic colour discrimination task. Exp Brain Res 1987; 66: 465-478.

118. Parthasarathy HB, Schall D, Graybiel AM. Distributed but convergent ordering of corticostriatal projections: Analysis of the frontal eye field and the supplementary eye field in the macaque monkey. J Neurosci 1992; 12: 4468-4488.

119. Petersen SE, Robinson DL, Keys W. Pulvinar nuclei of the behaving rhesus monkey: Visual responses and their modulation. J Neurophysiol 1985; 54: 867-886.

120. Petersen SE, Robinson DL, Morris JD. Contributions of the pulvinar to visual spatial attention. Neuro-psychologia 1987; 25: 97-105.

121. Pigarev IN, Rizzolatti G, Scandolara C. Neurons responding to visual stimuli in the frontal lobe of macaque monkeys. Neurosci Lett 1979; 12: 207-212.

122. Posner M. Orienting of attention. Q J Exp Psychol 1980; 32: 3-25.

123. Rayner K, ed. Eye Movements and Visual cognition: Scene Perception and Reading. New York: Springer-Verlag, 1992.

124. Remington RW. Attention and saccadic eye movements. J Exp Psychol: Human Percept Perform 1980; 6: 726-744.

125. Reuter-Lorenz PA, Fendrich R. Oculomotor readiness and covert orienting: Differences between central and peripheral precues. Percept Psychophys 1992; 52: 336-344.

126. Robinson DA, Fuchs AF. Eye movements evoked by stimulation of frontal eye fields. J Neurophysiol 1969; 32: 637-648.

127. Robinson DL, Goldberg ME, Stanton GB. Parietal association cortex in the primate: Sensory mechanisms and behavioral modulations. J Neurophysiol 1978; 41: 910-932.

128. Robinson DL, McClurkin JW. The visual superior colliculus and pulvinar. In: Wurtz RH, Goldberg ME, eds, The Neurobiology of Saccadic Eye Movements. New York: Elsevier, 1989: 337-360.

129. Robinson DL, Petersen SE. The pulvinar and visual salience. TINS 1992; 15: 127-132.

130. Rolls ET, Tovee MJ. Processing speed in the cerebral cortex and the neurophysiology of visual masking. Proc Roy Soc Lond B 1994; in press.

131. Saito H, Yukie M, Tanaka K, Kikosaka K, Fukada Y, Iwai E. Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. J Neurosci 1986; 6: 145-157.

132. Schall JD. Neuronal activity related to visually guided saccades in the frontal eye fields of rhesus monkeys: Comparison with supplementary eye fields. J Neurophysiol 1991; 66: 559-579.

133. Schall JD. Neuronal activity related to visually guided saccadic eye movements in the supple-mentary motor area of rhesus monkeys. J Neurophysiol 1991; 66: 530-558.

134. Schall JD. Neuronal basis of saccadic eye movements. In: Leventhal AG, ed, The Neural Basis of Visual Function. London: Macmillan Press, 1991: 388-442 (Cronly-Dillon J, ed, Vision and Visual Dysfunction, volume 4).

135. Schall JD, Hanes DP. Neural basis of saccade target selection in frontal eye field during visual search. Nature 1993; 366: 467-469.

136. Schall JD, King DJ, Morel A. Topography of afferents to frontal eye field (FEF) from the superior temporal sulcus (STS). Soc Neurosci Abstr 1993; 19: 1592.

137. Schall JD, Morel A, Kaas JH. Topography of supplementary eye field afferents to frontal eye field in macaque: Implications for mapping between saccade coordinate systems. Visual Neurosci 1993; 10: 385-393.

138. Schall JD, Morel A, King DJ, Bullier J. Topography of visual cortex connections with frontal eye field in macaque: Functional convergence and segregation of processing streams. J Neurosci 1995, in press.

139. Schall JD, Morel A, King DJ, Whalley C. Topography of connections between cortical visuomotor areas in the macaque. Soc Neurosci Abstr 1991; 17: 857.

140. Schiller PH. The effects of V4 and middle temporal (MT) area lesions on visual performance in the rhesus monkey. Visual Neurosci 1993; 10: 717-746.

141. Schiller PH, Logothetis NK. The color-opponent and broad-band channels of the primate visual system. TINS 1990; 13: 392-398.

142. Schiller PH, Sandell JH, Maunsell JHR. The effect of frontal eye field and superior colliculus lesions on saccadic latencies in the rhesus monkey. J Neurophysiol 1987; 57: 1033-1049.

143. Schiller PH, Stryker M, Cynader M, Berman N. Response characteristics of single cells in the monkey superior colliculus following ablation or cooling of visual cortex. J Neurophysiol 1974; 37: 181-194.

144. Schiller PH, True SD, Conway JD. Deficits in eye movements following frontal eye field and superior colliculus ablations. J Neurophysiol 1980; 44: 1175-1189.

145. Schlag J, Schlag-Rey M. Evidence for a supplementary eye field. J Neurophysiol 1987; 57: 179-200.

146. Schalg-Rey M, Schlag J, Dassonville P. How the frontal eye field can impose a saccade goal on superior colliculus neurons. J Neurophysiol 1992; 67: 1003-1005.

147. Schlag-Rey M, Schlag J, Sanchez H. FEF neurons activity during monkey performance of antisaccade tasks. Soc Neurosci Abstr 1993; 19: 785.

148. Schnyder H, Reisine H, Hepp K, Henn V. Frontal eye field projection to the paramedian pontine reticular formation traced with wheat germ

149. Segraves MA. Activity of monkey frontal eye field neurons projecting to oculomotor regions of the pons. J Neurophysiol 1992; 68: 1967-1985.

150. Segraves MA, Goldberg ME. Functional properties of corticotectal neurons in the monkey's frontal eye fields. J Neurophysiol 1987; 58: 1287-1419.

151. Shepherd M, Findlay JM, Hockey RJ. The relationship between eye movements and spatial attention. Q J Exp Psychol 1986; 38A: 475-491.

152. Sparks DL, Hartwich-Young R. The deep layers of the superior colliculus. In: Wurtz RH, Goldberg ME, eds, The Neurorbiology of Saccadic Eye Movements. Amsterdam: Elsevier, 1989: 213-255.

153. Sparks DL, Mays LE. Signal transformations required for the generation of saccadic eye movements. Ann Rev Neurosci 1990; 13: 309-336.

154. Stanton GB, Bruce CJ, Goldberg ME. Topography of projections to the frontal lobe from the macaque frontal eye field. J Comp Neurol 1993; 330: 286-301.

155. Stanton GB, Goldberg ME, Bruce CJ. Frontal eye field efferents in the macaque monkey: I. Subcortical pathways and topography of striatal and thalamic terminal fields. J Comp Neurol 1988; 271: 473-492.

156. Stanton GB, Goldberg ME, Bruce CJ. Frontal eye field efferents in the macaque monkey: II. Topography of terminal fields in midbrain and pons. J Comp Neurol 1988; 271: 493-506.

157. Suzuki H, Azuma M. Prefrontal neuronal activity during gazing at a light spot in the monkey. Brain Res 1977; 126: 497-508.

158. Suzuki H, Azuma M. Topographic studies on visual neurons in the dorsolateral prefrontal cortex of the monkey. Exp Brain Res 1983; 53: 47-58.

159. Tanaka K. Neuronal mechanisms of object recognition. Science 1993; 262: 685-688.

160. Tanaka K, Saito H-A, Fukada Y, Morriya M. Coding visual images of objects in the inferotemporal cortex of the macaque monkey. J Neurophysiol 1991; 66: 170-189.

161. Teuber H-L, Battersby WS, Bender MB. Changes in visual searching performance following cerebral lesions. Am J Physiol 1949; 159: 592.

162. Thompson KG, Hanes DP, Tu FF, Schall JD. Evolution of saccade target selection signal in frontal eye field during visual search. Soc Neurosci Abstr 1993; 19: 27.

163. Thorpe SJ, Celebrini S, Trotter Y, Imbert M. Dynamics of stereo processing in area V1 of the awake primate. European J Neurosci 1991; 4: S83.

164. Tovee MJ, Rolls ET, Treves A, Bellis RP. Information encoding and the responses of single neurons in the primate temporal visual cortex. J Neurophysiol 1993; 70: 640-654.

165. Treisman A. Features and objects: The Fourteenth

Bartlett Memorial Lecture. Q J Exp Psychol 1988; 40A: 201-237.

166. Ungerleider LG, Gaffan D, Pelak VS. Projections from inferior temporal cortex to prefrontal cortex via the uncinate fascicle in rhesus monkeys. Exp Brain Res 1989; 76: 473-484.

167. Ungerleider LG, Mishkin M. Two cortical visual systems. In: Ingle DJ, Goodale MA, Mansfield RJW, eds, Analysis of Visual Behavior. Cambridge: MIT Press, 1982: 549-586.

168. van der Heijden AHC. Visual information processing and selection. In: Neumann O, Prinz W, eds, Relationships between Perception and Action. Berlin: Springer-Verlag, 1990.

169. van Gisbergen JAM, Van Opstal AJ. Models. In: Wurtz RH, Goldberg ME, eds, The Neurobiology of Saccadic Eye Movements. Amsterdam: Selsevier, 1989: 69-101.

170. van Gisbergen JAM, van Opstal AJ, Tax AAM. Collicular ensemble coding of saccades based on vector summation. Neurosci 1987; 21: 541-555.

171. van Opstal AJ, van Gisbergen JAM. A nonlinear model for colliculus spatial interactions underlying the metrical properties of electrically elicited saccades. Biol cybernet 1989; 60: 171-183.

171a. van Opstal AJ, van Gisbergen JAM. Role of monkey superior colliculus in saccade averaging. Exp Brair Res 1990; 79: 143-149.

172. Viviani P. Eye movements in visual search: Cognitive, perceptual and motor control aspectds. In: Kowler E, ed, Eye Movements and their Role in Visual and Cognitive Processes. Amsterdam: Elsevier Science Publishers BV (Biomedical Division), 1990: 353-393.

173. Viviani P, Swensson RG. Saccadic eye movements to peripherally discriminated visual targets. J Exp Psychol: Hum Percept Perform 1982; 8: 113-126.

174. Vogels R, Organ GA. How well do response changes of striate neurons signal differences in orientation: A study in the discriminating monkey. J Neurosci 1990; 10: 3543-3558.

175. Vogels R, Organ GA. Quantitative study of striate single-unit respolnses in monkeys performing an orientation discrimination task. Exp Brain Res 1991; 84: 1-11.

176. von der Heydt R, Peterhans E. Mechanisms of contour perception in monkey visual cortex. I. Lines of pattern discontinuity. J Neurosci 1989; 9: 1731-1748.

177. Wise SP. The primate premotor cortex: Past, present and preparatory. Ann Rev Neurosci 1985; 8: 1-19.

178. Wolfe JM, Cave KR. Deploying visual attention: The guided search model. In: Blake Aa, Torscianko T, eds, AI and the Eye. New York: John wiley & sons, 1990: 79-103.

179. Wurtz RH, Goldberg ME, eds, The Neurobiology of Saccadic Eye Movements. New York: Elsevier, 1989.

180. Wurtz RH, Mohler CW. Enhancement of visual responses in monkey striate cortex and frontal eye fields. J Neurophysiol 1976; 39: 766-772.

181. Wurtz RH, Mohler CW. Organization of monkey superior colliculus: Enhanced visual response of superficial layer cells. J Neurophysiol 1976; 39: 745-765.

182. Yarbus AL. Eye Movements and Vision. New York: Plenum Press, 1967.

183. Young MP. Objective analysis of the topological organization of the primate cortical visual system. Nature 1992; 358: 152-154.

184. Zohary E, Hillman P, Hochstein S. Time course of perceptual discrimination and single neuron reliability. Biol cybernet 1990; 62: 475-486.