VISUOSPATIAL AND MOTOR ATTENTION IN THE MONKEY

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Abstract—Visuospatial attention involves the selection of stimuli from the environment for further neural processing. The attention-related enhancement of visual responses in posterior parietal cortex is a possible neural substrate for visuospatial attention. By analogy with the selection process in the spatial domain, motor attention is postulated to involve a selection among simultaneous upper motor signals. Selection of motor programs within the oculomotor system is used as an example of this attentional process. Since attentive fixation modulates the effect on the oculomotor system of electrical stimulation of the frontal eye fields, a given upper motor neuronal signal need not necessarily invoke a movement. That the brain has multiple simultaneous motor signals is apparent from the profusion of sensory-driven upper motor neurons. The frontal cortex is probably important in selecting which upper motor signals actually evoke movements, by elaborating motor programs for purposive behavior, but not for all movements.

ATTENTION has been defined since the nineteenth century as the process by which the brain selects one or more objects from the environment for further analysis [15]. This process has been studied most actively in the spatial realm, where the selection process of visual attention has been examined in human and animal models [22, 29]. Behavioral enhancement of neuronal responses to visual stimuli has been suggested as a neural substrate for visuospatial attention. The choice of an attended stimulus is facilitated by the enhanced responses of sensory neurons to that stimulus [3]. However, the brain must also make a different set of choices: it must choose among a series of plausible and perhaps conflicting motor programs to order its behavior. Clearly the process invoked by the teacher when she pleads to her wayward student to “pay attention” includes this latter process: she is asking her student to choose the most efficient series of behaviors from among a welter of potential activities. There are at least two possibilities for the organization of this choice. The first is that the organism selects behaviors and initiates the neural signals for the requisite movement de novo. Another possibility is that there is a multiplicity of actual upper motor signals in the brain at any given time, and the ordering of behavior is to some extent an attentional process that chooses among these preexisting signals. This process would be analogous to spatial attention, entailing a choice among conflicting internal motor signals rather than among conflicting external stimuli in the environment. This brief review will begin by discussing the processes of spatial attentional selection as illustrated by the process of enhancement of sensory responsiveness in the visual system of the monkey, and then discuss the evidence for its analog in the motor-behavioral domain.

PRESACCADIC ENHANCEMENT OF VISUAL RESPONSES

GOLDBERG and WURTZ [10] first noted that visual responses in the monkey superior colliculus were dependent upon both the physical properties of a stimulus and its behavioral
significance. They noticed that when a monkey made a saccade to a visual target, that target evoked a brisker response in neurons in the superficial layers of the superior colliculus than when the monkey performed a fixation task in which it did not make a saccade to the stimulus in the receptive field. These neurons were in fact discharging in response to the stimulus. They had no activity before saccades made without visual targets, and since the enhancement occurred before the saccade it could not be due to some artifact of movement alone. In fact, many of the cells which showed presaccadic enhancement also showed suppression of their activity by the saccade itself. The enhancement was selective to saccades made to the stimuli in the receptive field, and did not occur before saccades made to stimuli elsewhere. It therefore could not have been related to the various non-specific events associated with saccadic eye movements, such as pupillary dilation or changes in the general level of arousal of the monkey. It had to be specifically related to the attentional processes preceding the saccade. Figure 1 shows an example of presaccadic enhancement in the monkey frontal eye fields, but a similar illustration could have been selected from neurons in the superior colliculus, the posterior parietal cortex [3], the prelunate cortex [6], or the pulvinar [21]. Figure 1A shows the response of a neuron when the monkey performs a fixation task and does not make a saccade to a stimulus in the receptive field. Figure 1B shows the unenhanced

![Presaccadic enhancement in the frontal eye fields.](image)

**FIG. 1.** Presaccadic enhancement in the frontal eye fields. Each illustration consists of cell activity on the left and a cartoon of the paradigm on the right. Cell activity is illustrated both as raster (left) and histogram (right). In the raster diagrams each dot represents a cell discharge. Each row represents a 2 sec epoch of cellular activity, and successive epochs are shown on successive lines, all synchronized on the appearance of a visual stimulus, depicted by the vertical trigger line. The histograms sum the activity in the rasters, with bin width of 12 msec. Vertical trigger corresponds to a spike frequency of 152 Hz. A shows the response of the neuron to two stimuli, one (RF) presented in the receptive field of the neuron (outlined) and the other (CON) outside the receptive field. B shows the response of the neuron to the appearance of the stimuli when both appear but the monkey makes a saccade to CON. C shows the response of the same neuron to the same stimuli when the monkey makes a saccade to RF. Note the enhanced response in C relative to A and B. Reproduced with permission from *Journal of Neurophysiology* [8].
response to the stimulus when the monkey makes a saccade to a control stimulus outside the receptive field, and Fig. 1C shows the enhanced activity of the neuron when the monkey makes a saccade to the stimulus in the receptive field. Therefore, the enhancement demonstrated in this neuron is specific to the stimulus in the receptive field, and could perform a selection of that stimulus for further neural processing.

ENHANCEMENT RELATED TO GENERAL VISUOSPATIAL ATTENTION

GOLDBERG and WURTZ [10] postulated that the presaccadic enhancement shown in the superior colliculus was a substrate for visual attention. However, although saccades are intimately related to visual attention, they can be separated from it. It was apparent that in order for the enhancement to be related to general visuospatial attention, it had to be present when the monkey attended to a stimulus but did not make a saccade to it. WURTZ and MOHLER [30] trained monkeys to respond either to a peripheral target or to a central fixation point without making a saccade to the peripheral target. Since the monkey responded to the stimulus they assumed that the animal had attended to it. They found that neurons in the superior colliculus did not yield an enhanced response to the stimulus in their receptive fields when the monkey attended to the stimulus without making a saccade to it. Thus, although presaccadic enhancement could have been a substrate for visuospatial attention it was not so in the superior colliculus.

The posterior parietal cortex does have attention-related enhancement of visual responses that is independent of saccades. Because of the neglect associated with right posterior parietal lesions in human patients, it has long been postulated [12] that the posterior parietal cortex was involved in the processes underlying visuospatial enhancement. HYVÄRINEN and PORANEN [14] and MOUNTCASTLE et al. [20, 17] showed that the posterior parietal cortex of the monkey had neurons which discharged in association with attentive saccades. ROBINSON et al. [24] showed that this activity was enhanced visual activity, and BUSHNELL et al. [3] demonstrated that this enhancement was independent of saccadic eye movements. They trained monkeys in two separate saccade-free attention tasks. In one the monkey had to signal when a peripheral stimulus dimmed without making a saccade to it; in the other the monkey had to reach out and touch the stimulus with its hand without making a saccade to the stimulus. Enhancement was found in saccade-free as well as saccade-requiring tasks, and in each case there was a high correlation between enhancement in a saccade task with enhancement in a saccade-free task. Figure 2 shows a neuron in the monkey posterior parietal cortex with a weak visual response (Fig. 2A) which is enhanced before a saccade (Fig. 2B) or before a peripheral attention saccade-free task (Fig. 2C). Both saccade-related and saccade-free enhancement in the posterior parietal cortex are spatially specific, and do not occur when the monkey attends to a stimulus outside the receptive field. The parietal cortex, therefore, has activity paradigmatic for visuospatial attention: when a stimulus is important to the animal, when it attends to it, that stimulus evokes a more intense response from parietal neurons. This process provides a neural substrate for the psychological process of attention.

THE SELECTION OF MOTOR PROGRAMS AS AN ATTENTIONAL PROCESS

The mechanism of selective enhancement of visual responses enables an organism to choose what stimulus in the environment is important, and then enables that stimulus to
provide the brain with a more powerful quantitative effect. By choosing among competing external alternatives the brain shapes the interaction of the organism with its environment. However, the organism navigating its way through a complex world also has to make a different series of choices, among competing motor programs and strategies of behavior. This review suggests the term motor attention for this process of choice to emphasize its similarity with the process of visuospatial attention.

The evidence that the organization of behavior consists to some extent in the choice among competing motor programs rather than the monolithic initiation of one program at a time comes from the analysis of cell types and the effects of electrical stimulation in the monkey frontal eye fields. BRUCE and GOLDBERG [1] studied the activity of monkey frontal eye field cells using a battery of tasks including a fixation task, a visually guided saccade task, and a learned saccade task. In this latter task the monkey learned to make a saccade of a certain amplitude and direction and then reliably made the saccade in total darkness, in response to the disappearance of a fixation point. Since there was no stimulation of the retina by a target, the monkey had to rely on its memory of where the target had been in previous trials. In the monkey frontal eye fields roughly 60% of all cells discharge before purposive, visually guided saccadic eye movements. Of these cells, 40% are visual cells, discharging in response to visual stimuli, but not before purposive saccades made in the learned saccade task. Twenty percent are movement cells, discharging as well before learned saccades as before visually guided saccades. These cells do not discharge before spontaneous saccades in total darkness. The remaining 40% are visuomovement cells, discharging best before visually guided saccades, but also before learned saccades made without visual stimuli and in response to visual stimuli presented in the presence of saccades. Figure 3 illustrates these three different types of frontal eye field neurons, discharging during a task in which the monkey has to look at a fixation point while a peripheral stimulus appears, but must hold fixation for a second, and only make a saccade to the stimulus when the fixation point disappears. The first cell is a visual cell, discharging in response to the stimulus appearance but not before the saccade (first row). The second cell is a visuomovement cell, responding to the appearance of the stimulus but
Fig. 3. Cell types in the frontal eye fields. Each diagram shows post-stimuli histograms synchronized on stimulus onset (left) and saccade onset (center) for a certain cell, and the behavior for a sample trial (right). In the behavioral diagrams, horizontal (H) and vertical (V) eye position as measured by the magnetic search coil technique, and fixation point (S1) and saccade target (S2) status are shown. In the paradigms shown, the target appears at the step in the S2 line, but the monkey cannot make the saccade before the fixation point disappears, at the downward step in the S1 line. In each trial the monkey was rewarded by making a saccade of proper direction and amplitude, as illustrated by the artifacts at the beginning and end of the saccade in the vertical position trace. Cell discharge in the sample trials is signified by the dots between the eye position and stimulus traces. The first cell (19-018) is a visual cell which responds to the stimulus (left histogram) but not the saccade (right histogram). The second cell (19-007) is a visuomovement cell which discharges both in response to the stimulus (left histogram) and before the saccade (right histogram). The discharge continues from stimulus to movement whether or not the stimulus remains on throughout the trial (second trace) or merely flashes for 50 msec and then disappears (third trace). The third cell (19-063) is a movement cell that does not respond to the stimulus (left histogram) but discharges before the saccade (right histogram). Reproduced with permission from the Journal of Neurophysiology [1].
maintaining its discharge until the saccade, whether or not the stimulus stays on the screen (second row) or flashes briefly and then disappears (third row). The third cell (fourth row) shows a movement cell that has no response to the stimulus but discharges before the saccade.

Stimulation of the frontal eye fields evokes contraversive eye movements [5, 23] and the properties of saccades evoked by electrical stimulation are correlated with the nature of the cells recorded at the stimulation site [2]. The amplitude and direction of the evoked saccades are similar to the amplitude and direction of the saccades associated with the briskest discharge of the cells, and the threshold of stimulation correlates with cell types, movement cells in general being associated with low thresholds (< 50 µamp) and visual cells with high ones (> 150 µamp). These data suggest that stimulation of the frontal eye fields results in the artificial activation of natural pathways. According to this hypothesis the superior colliculus and pontine reticular formation, recipients of frontal eye field efferents [16] should not be able to distinguish activation of premotor neurons by natural events and activation of the same neurons by electrical stimulation. Phenomena associated with electrical stimulation should hold to some extent for phenomena associated with true neural activity.

Goldberg et al. [9] have recently demonstrated that attentive fixation affects the eye movements evoked by electrical stimulation of the frontal eye fields. They compared the results of electrical stimulation of the monkey frontal eye fields during two different behaviors in which the eye was still in the center of the orbit. In one case the monkey was actively fixating a spot of light, either waiting to signal when the light might dim or actively holding its eyes in the location of the light waiting for a reward. In the other case the monkey was alert but performing no task. The computer chose epochs in which the eye was still in the center of the orbit. There are two effects of attentive fixation: an elevation of the threshold for evoking saccades and a lowering of the amplitude and velocity of saccades so elicited. Figure 4 shows the threshold effect, illustrating the probability of evoking any saccade at a
given current in the attentive fixation (closed circles) and rest (open circles) cases. Note that
at currents between 30 and 50 μ amps, stimulation which can evoke a saccade at rest cannot
evoke a saccade during attentive fixation. The effect is one of receptiveness of the oculomotor
system to frontal stimulation rather than responsiveness of the frontal eye fields to electrical
stimulation, since stimulation in the white matter underlying the frontal eye fields had the
same effect as the grey matter stimulation illustrated here.

When saccades are evoked they are slower and shorter, as can be seen in Fig. 5. Figure 5A
shows the amplitudes of saccades evoked from suprathreshold currents at three different
sites. Figure 5B shows the radial velocity/radial amplitude relationships for the saccades
illustrated in 5A. In each case the open symbols depict fixation trials and closed symbols
depict rest trials. The results show that both the mean amplitude and mean velocity are
decreased by attentive fixation. Saccade direction is slightly affected in that longer saccades
tend to be slightly more horizontal.

![Graph A](image1)

![Graph B](image2)

Fig. 5. Characteristics of saccades evoked by electrical stimulation of the monkey frontal eye fields
during attentive fixation (open symbols) and rest (closed symbols). Same stimulation parameters are
as in Fig. 4. A shows eye position at end of saccades (abscissa horizontal position, ordinate vertical
eye position) for three different stimulation sites. B shows the radial velocity as a function of saccade
radial amplitude for the saccades illustrated in A. Reproduced with permission from Experimental
Brain Research [9].
The shorter, slower saccades could arise because the attentively fixating monkey brakes the saccade in mid-flight, or because the system programs a smaller saccade. The latter is more likely because phase-plane analysis of saccade trajectories reveals that the shorter saccades evoked by electrical stimulation during attentive fixation have the patterns of normal short saccades, and can be distinguished from the longer saccades evoked by electrical stimulation as soon as 8 msec after the beginning of the saccade. If the saccade were rapidly braked then one would expect the early part of the saccade initiation pattern to resemble the longer saccades. These data show that the elaboration of motor programming involves modifying the expression of premotor signals according to the monkey's behavioral state, since presumably the signals evoked from the frontal eye fields by electrical stimulation are more likely to be real neuronal signals from the neurons illustrated above than electrical artifacts. The premotor signals can issue from areas as close to the final motor pathways as the frontal eye fields or the superior colliculus, in which Sparks and Mays [26] have demonstrated a similar effect of attentive fixation on the saccades evoked by electrical stimulation. Thus nuclei a few synapses away from the extraocular muscles do not issue obligate commands to the saccadic system, but rather signals among which the system can select.

AMBIGUOUS SIGNALS AND MOTOR NOISE

The central hypothesis of this review is that the motor system performs an attentional process by choosing among pre-existing motor command signals. The above experiment uses an electrically evoked saccade signal and an internal fixation signal as two competing signals. In order for the hypothesis to be true, however, there must be evidence for the existence of simultaneous contradictory motor signals in the normal brain. There are at least two different candidates for such a tentative motor signal: neurons with both sensory and motor components to their discharge, and neurons with motor signals that are not necessarily followed by motor events. Both of these signals have been demonstrated in the superior colliculus and the frontal eye fields.

In the intermediate layers of the superior colliculus there are neurons which discharge both in response to visual stimuli in the absence of movements, and also before saccades in the absence of stimuli, even spontaneous saccades in total darkness [28]. Meredith and Stein [18] have reported trimodal neurons in the deep layers of the cat superior colliculus, neurons that discharge in response to somatosensory, acoustic, and visual stimuli, and although they have not recorded from these neurons in awake animals, they have postulated that these neurons are involved in orientation of eye, pinna, and head. Similar multimodal neurons are found in the frontal eye fields: both the visuomovement neurons described above, with concurrent visual and movement signals, and a class of neurons that has both presaccadic and postsaccadic activity. A neuron of this sort is shown in Fig. 6. It discharges before saccades upward to right and after saccades downward to the left. Each discharge obeys the rules of its own type: the presaccadic activity occurs before purposive activity but not before spontaneous saccades in the dark; the postsaccadic activity is similar after both purposive and spontaneous saccades. Electrical stimulation at the site of this neuron results in a saccade in the presaccadic direction.

These multimodal neurons have an ambiguous message. It could be decoded as a post-event signal: "there is a visual stimulus" or as pre-event signal: "make a saccade". Interpreting the signal carried by such ambiguous neurons is easy for the physiologist, who
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PRE-SACCADIC DIRECTION
(trigger line = saccade start)

POST-SACCADIC DIRECTION
(trigger line = saccade end)

Visually Guided Saccades

Spontaneous Saccades in Dark

Electrically Elicited Saccades

Fig. 6. Comparison of neuronal activity and the saccade evoked by electrical stimulation near a cell with pre- and post-saccadic activity in the monkey frontal eye fields. Each diagram shows representative eye position traces and histogram and rasters synchronized on the beginning of the saccade. In the eye position traces the horizontal component is shown above the vertical component. Activity is shown for both pre-saccadic (left column) and post-saccadic (right column) optimum directions for visually guided saccades (top) and spontaneous saccades in total darkness (bottom). Sample saccades evoked by electrical stimulation are shown at the bottom. Reproduced by permission of the Journal of Neurophysiology [2].

presents a stimulus or measures a behavior, and then correlates cell discharge with the event. However, for the neuron or neuronal system to which this cell projects the problem is not so easy. The neuron is faced with at least two different solutions for the ambiguity. The first is to assume that the neuronal message arrives in parallel with an unambiguous signal. The recipient system knows that the signal means "a downward to the left eye movement has just occurred" because the unambiguous signal says so; but in this case what purpose does the ambiguous signal serve since the unambiguous message is already present? The second
solution is that the recipient system interprets all signals unambiguously, as one message regardless of the evoking event. Thus the discharge of sensorimotor cells of the frontal eye fields and the superior colliculus would always be interpreted as motor signals and never as sensory signals. Because of the motor interpretation of the sensory signal, a visual stimulus would automatically evoke the motor signal needed to acquire it by a saccade, and a saccade would automatically evoke the motor signal needed to bring the eye back to the original fixation point. The recipient region would not necessarily have access to the actual event evoking the signal, which might be a visual stimulus, a sound, another saccade, or even some stimulus-free event. However, the motor system does not need any information about the sensory or internal reason for its movement; all it needs is targeting and triggering signals. This means that the motor region constantly receives a number of signals all of which are interpreted as motor commands. All events which could evoke activity in sensorimotor neurons do not necessarily evoke movement. We do not make saccades to every light or sound, nor do we reverse every saccade; nonetheless every saccade and every light or sound evokes a motor signal which arrives at quite low levels in the nervous system. This superfluity of motor commands suggests that the motor system lives in a noisy environment, and that the absence of a purposive selection system results in extraneous movement rather than no movement.

Another kind of motor noise can be seen in the activity of neurons in the intermediate layers of the superior colliculus. These neurons discharge before all saccades, but if one examines their activity one can see bursts which do not precede actual saccades, even though these bursts may be as intense as those followed by movements. Thus although a saccade implies that a burst has occurred, a burst increases the probability of a saccade but does not necessarily force one [19].

Whether or not those motor signals were actually converted to movement would be determined by the selection process described above as motor attention. If the animal were engaged in meaningful action, for example attentive fixation, the signal would be less likely to evoke a movement than if the animal were alert and at rest. The presence of sensory-evoked and spontaneous motor signals ensures that in the absence of some purposive motor plan there are many signals that evoke movement. It also explains why seemingly purposeless movements occur: for example, the eye movements humans make during mental arithmetic or in total darkness. These movements are not part of a significant motor scheme, and they are not associated, for example, with a large frontal eye field signal, but they may occur because there is no reason not to select them.

THE FRONTAL CORTEX AS A CANDIDATE FOR A SELECTOR OF MOTOR STRATEGIES

The mechanism of selection of motor strategies is not clear, but there is evidence, predominantly behavioral, that the frontal cortex is important for the selection process [7]. To cite examples from the oculomotor system, Guitton et al. [11] tested humans with unilateral frontal excisions for intractable epilepsy on a task which required that they look away from a stimulus. They found that the patients had great difficulty suppressing saccades to the stimulus when it lay in the field contralateral to the lesion. Deng et al. [4] found that monkeys with unilateral frontal eye field ablations had difficulty making memory guided saccades to targets that appeared and disappeared while they were looking at a fixation point. One type of error the monkeys frequently made was to make a saccade to the target
while it was still present, even though the fixation point had not yet disappeared. Both of these errors are stimulus-bound: the proper behavior is to refrain from making a saccade to a stimulus when it appears, but the monkeys and humans with frontal lesions could not suppress the unwanted behavior. In the absence of a frontal eye field the motor signal evoked by the stimulus in sensorimotor cells must have been sufficient to evoke the movement.

The neural mechanism by which this selection of motor programs takes place must be quite complicated. It cannot simply be that the frontal eye field saccadic mechanism directly suppresses lower centers because a purely suppressive signal would be expected to show a high spontaneous firing rate except around saccades, at which time it would be expected to be silent. Such a discharge pattern has never been observed in the frontal eye fields, although it has been found in the substantia nigra by Hikosaka and Wurtz [13]. A more likely candidate for the mechanism is that the frontal eye fields project downward signals for most important oculomotor behaviors: fixation, [27, 1] saccades [1], and even smooth pursuit [2]. This is supported by evidence that cells with these motor signals project to the superior colliculus, but cells with purely visual activity do not [25]. Thus fixation activity in the frontal fixation system could serve to suppress saccadic systems, and the sorts of activity that could induce a saccade in the absence of the frontal fixation signal would not be able to do so in its presence. The oculomotor system would express the motor program originating from the frontal cortex. In the absence of a frontal signal more primitive stimulus-evoked or spontaneous motor signals would be sufficient to evoke the movement.

The motor program dictated by prefrontal processing should be the most compelling for all motor systems. The tendency of monkeys and humans with frontal lesions to be overly stimulus-bound bear this out, since these organisms are more susceptible to the motor signals evoked by sensory stimuli or internal motor noise. In the absence of a frontal signal, for example when a monkey is in the dark and has no oculomotor task, the eyes do not remain still; instead, other motor signals take control of the saccadic system since there is no concurrent frontal activity. However, when a form of behavior becomes important to an organism, for example a visually guided saccade crucial to the animal's ongoing behavior, then frontal motor signals would take control of the system, and adventitious signals would not result in behavior. The selection of an appropriate motor signal in the presence of conflicting motor signals is thus an analog of the selection of appropriate sensory stimuli in the external world, and this review postulates that the selection of behavior is a motor attentional process analogous to the process of visuospatial attention.

REFERENCES