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The dorsomedial frontal cortex of the macaca monkey: fixation and saccade-related activity

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Summary. The activity of 249 neurons in the dorsomedial frontal cortex was studied in two macaque monkeys. The animals were trained to release a bar when a visual stimulus changed color in order to receive reward. An acoustic cue signaled the start of a series of trials to the animal, which was then free to begin each trial at will. The monkeys tended to fixate the visual stimuli and to make saccades when the stimuli moved. The monkeys were neither rewarded for making proper eye movements nor punished for making extraneous ones. We found neurons whose discharge was related to various movements including those of the eye, neck, and arm. In this report, we describe the properties of neurons that showed activity related to visual fixation and saccadic eye movement. Fixation neurons discharged during active fixation with the eye in a given position in the orbit, but did not discharge when the eye occupied the same orbital positions during nonactive fixation. These neurons showed neither a classic nor a complex visual receptive field, nor a foveal receptive visual field. Electrical stimulation at the site of the fixation neurons often drove the eye to the orbital position associated with maximal activity of the cell. Several different kinds of neurons were found to discharge before saccades: 1) checking-saccade neurons, which discharged when the monkeys made self-generated saccades to extinguish LED's; 2) novelty-detection saccade neurons, which discharged before the first saccade made to a new visual target but whose activity waned with successive presentations of the same target. These results suggest that the dorsomedial frontal cortex is involved in attentive fixation. We hypothesize that the fixation neurons may be involved in codifying the saccade toward a target. We propose that their involvement in arm-eye-head motor-planning rests primarily in targeting the goal of the movement. The fact that saccade-related neurons discharge when the saccades are self initiated, implies that this area of the cortex may share the control of voluntary saccades with the frontal eye fields and that the activation is involved in intentional motor processes.

Key words: Dorsomedial frontal cortex – Fixation neurons – Checking saccades neurons – Novelty detection neurons – Activation – Monkey

Introduction

The dorsomedial frontal cortex is also named area 6aβ (Vogt and Vogt 1919) or FC and part of FB (Von Bonin and Bailey 1947) and is an area involved in eye movements. Mott and Schaefer (1890) found that electrical stimulation of this area in the monkey resulted in eye movements in the contralateral direction. The dorsomedial frontal cortex is the superior part of the premotor area (area 6 described by Brodmann 1905). This area has been reported to be involved in three functions: 1) in the control of movement in response to sensory stimuli; 2) in the preparation for and execution of movement (Kubota and Hamada 1978; Halsband and Passingham 1982; Weinrich and Wise 1982; Godschalk and Lemon 1983; Weinrich et al. 1984; Godschalk et al. 1985; Wise and Mauritz 1985) and 3) in attentional processes (Rizzolatti et al. 1983).

For some years, researchers have been studying the involvement of this area in motor processes. Schlag and Schlag-Rey (1987a) showed that this area contains a region where neurons are related to spontaneous and visually guided saccades. Mann et al. (1988) suggested that the cells here are involved in motor-learning processes. Rizzolatti et al. (1990) suggested that the area is involved in reaching-grasping arm movements. We (Bon and Lucchetti 1990, 1991) found cells whose activity was related to maintenance of attentive fixation as well as cells whose activation was related to coordinated eye and arm movements.

The aim of the present research was to investigate the role played by the dorsomedial frontal cortex in oculo-

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motor processes. We were particularly interested in any possible distinctions between cells active before saccadic eye movements and those involved in visual fixation.

Methods

Behavioral methods

The experiments were carried out on two macaque monkeys (one Macaca nemestrina and one Macaca fascicularis) trained on fixation and saccade tasks. Each monkey learned to press a bar to illuminate a bicolored light-emitting red/green diode (LED, SIEMENS LS110). After a random time (0.5–5.0 s), the LED turned from red to green for a fixed period of time (0.5 s). The animal had to release the bar during the green period to receive a liquid reward.

Preliminary training was done with the apparatus mounted on the monkey's home cage. After the monkey learned to perform this fixation task in the cage, it was taught to sit in a primate chair and perform a saccade task. In this task one of several LED's could be switched on in red mode, and subsequently switched to green to serve as a reward cue. The original fixation LED switched off

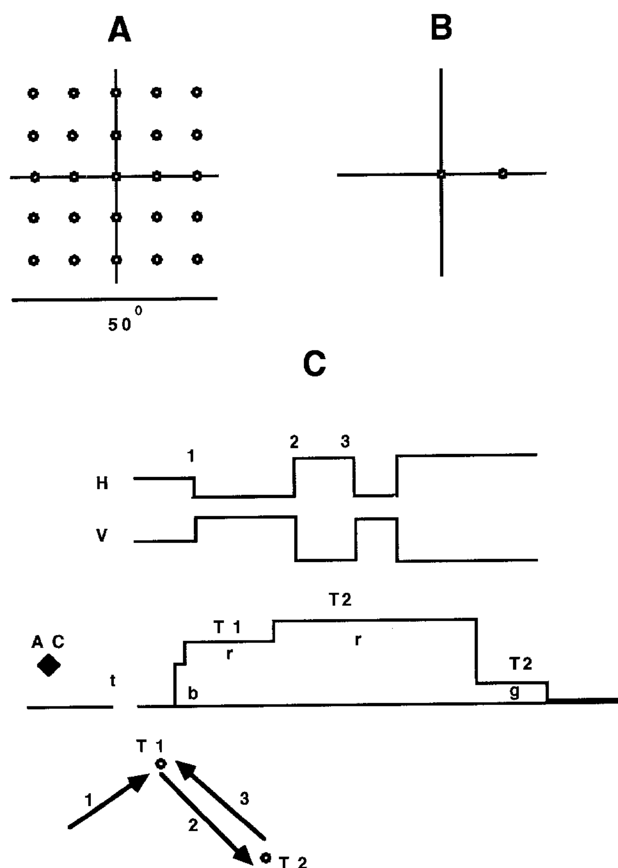

Fig. 1A–C. Diagrams of stimulus arrays and task paradigm. **A** and **B** Representation of the array with 25 LEDs and with 2 LEDs. The LEDs could be moved in all positions of the plane in front of the animal. **C** Is a representation of the paradigm with 2 LEDs T1 and T2. In the diagram, an extra saccade (3) is represented. H, V: horizontal and vertical components of eye position; 1 and 2: visual guided saccades; 3: extra saccade (checking saccade) self initiated; AC: acoustic cue; t: the free period in which the animal can press the bar without time limits; b: bar press; r: red period; g: green period; T1 and T2: targets

simultaneously with the onset of the second LED. An acoustic cue marked the start of the task; the animal was then free to begin the trials at will. The acoustic cue remained on throughout the series of trials and switched off at the end. The LED's, which were 0.05 deg in diameter, were positioned 200 cm in front of the monkey and featured two basic arrays: one with twenty-five targets and one with only two targets (Fig. 1A, B). We were able to test the visual field, with a resolution of one degree, by moving the targets in all positions of the visual field. The extent of the visual field tested was 50 deg (± 25) in the horizontal axis and 50 deg (± 25) in the vertical axis.

The trial was not aborted if the animal made an extra saccade (Fig. 1C). We observed that the animal often made saccades apparently to check the status of the unlit targets in the two-LED task (Fig. 1C, 3). The monkeys made these checking saccades spontaneously, without any reward or punishment. We considered such saccades self-initiated, probably because the monkey disliked losing the reward.

After the monkeys learned to perform the saccade task, they were prepared for the eye position measurement and head restraint. After a week, the monkeys were trained with the head fixed in place until they performed the saccade task successfully at a level of 90–100% (Macaca nemestrina) and 70–80% (Macaca fascicularis). Then the animals were prepared for the recording of unit activity.

We studied unit activity under the following conditions:

1) Fixations and saccades with an array of twenty five LEDs in both the dark and the light

2) Saccades with an array of two LEDs in both the dark and the light

3) Spontaneous saccades without LEDs in both the dark and the light

4) Scanning saccades with complex patterns.

Surgical methods

The monkeys were anesthetized with ketamine (10 mg per kg i.m.) and maintained with intravenous thiopental sodium. One hollow stainless steel cylinder was attached to the skull with four screws (Evarts 1968) and cemented in place (Refobacin-Palacos R Bracco) to allow a painless fixation of the head. Using aseptic techniques, we implanted a search coil subconjunctivally (Judge et al. 1980). Four stainless-steel wires were inserted into the neck muscles to monitor EMG. A stainless-steel chamber for recording the activity of single cells was implanted vertically over each hemisphere.

Physiological and data analytical methods

Eye movements were recorded by the search coil technique using the phase detection method (Remmel 1984). Single neurons were isolated with epoxilite-coated tungsten electrodes that were advanced through the dura with a hydraulic microdrive (Narishige MO-95B). The microelectrode signal was amplified (Bak MDA-4), it passed through a custom-built band-pass filter (500–7500 Hz) to eliminate artifacts from the 50 and 75 KHZ coil drivers. Then it passed through a window discriminator (WPI 121) that generated unit pulses to be sampled by the computer. The EMG activity of the neck muscles was used to monitor the animal's attempts toward head rotation. The cells were tested with classical visual stimuli (such as bars and dots) and with complex, motivational visual stimuli (such as colored boxes, gloves, brooms and pieces of fruit).

Electrical stimulation was induced using a two channel stimulator (WPI 302–T) connected to two constant-current stimulus isolation units (WPI 305–2R) wired to provide biphasic square wave pulses. The pulse duration was 0.25 ms per phase; the stimulation frequency was 330 Hz, and the train duration 70–100 ms. The current usually ranged from 8 to 50 μA, and never went over 150 μA.

The eye position, bar state (pressed or released), LED state, and unit activity were sampled at 1 KHZ and stored by a computer (Digital Equipment MINC 11/73). The signals were analyzed off-

line by a graphic unit (Tesak VDC 501). The animal's behavior was monitored by an infrared closed-circuit television system and recorded on videotape for further controls. Coagulation marks were made by a DC current (10 μA for 10 s) at some of the recording sites for histological reconstruction. At the end of the experiments, the animals were anesthetized with a large dose of pentobarbital and perfused with 0.9% of a NaCl solution followed by 5% of formalin. Subsequently, the brain was sectioned into 60 μ coronal slices and stained with thionine.

Results

We recorded the activity of 249 neurons. Of these cells, 157 neurons, recorded in 49 penetrations, discharged in relation to either eye, neck, ear, eyelid, or arm movement (Table 1).

We did not see a strict segregation of these different functions in different areas; instead, we found that neurons related to arm- and eye-movement were distributed throughout the region of the dorsomedial frontal cortex that we studied (Fig. 2). As described below, the electrical stimulation at the oculomotor sites frequently evoked eye movements. Using currents up to 150 μA we were unable to evoke arm movements from any site. During any given penetration, the cells encountered usually had different functions; this effect may be attributed to the angle of the microelectrode in the cortex.

Table 1. Different types of neurons recorded and their percentage distribution

Eye	97 (62%)
Arm	36 (23%)
Neck	5 (3%)
Eyelid	4 (2%)
Ear	15 (10%)
TOT.	157 (100%)

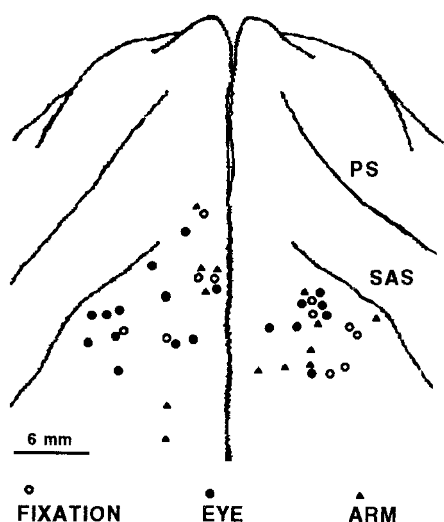

Fig. 2. Mapping of the penetrations in both monkeys. Dorsal view of the frontal pole of the monkey brain: PS principal sulcus, SAS superior arcuate sulcus. This figure represents 43 penetrations of the 49; six penetrations are overlapped. Each mark symbolizes the penetrations where fixation as well as eye and arm neurons have been found. In the same penetration we could find cells with similar or different features. This result might be explained by the angle of the electrode with the cortex

Oculomotor cells

The cells related to eye movements were found throughout the DMFC as well as rostrally on the border of area

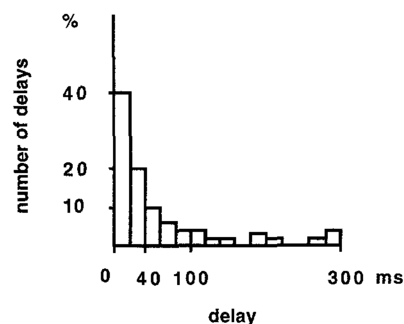

Fig. 3. Percent distribution of the discharge delays in the fixation neurons after saccades. The delay was studied in fifteen cells for ten trials each

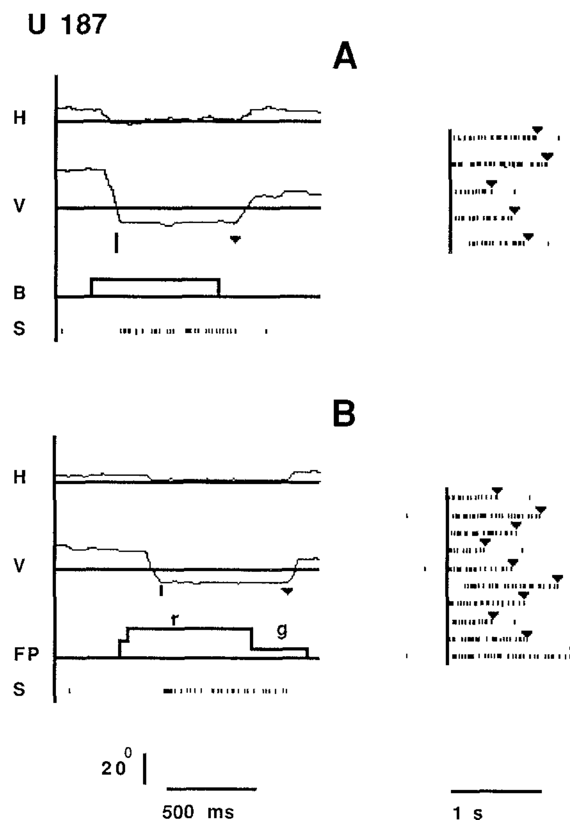

Fig. 4A, B. Comparative examples of the same cell discharging during the rest period **A** and during the task **B** for the same eye position. The discharge was weak during free gazing, rest period A while it was brisk during fixation, task condition **B**. The position of the eye was the same in both conditions, but in B the attention was engaged. H: horizontal component of the eye position; V: vertical component of the eye position; FP: fixation point; r: red period; g: green period; S: spikes; each dot represents one spike. The rasters are synchronized with the onset of fixation. The triangles represent the end of the fixation

9 (Vogt and Vogt 1919). Of these oculomotor cells, twenty-five percent (25/97) were related to eye fixation and seventy-two percent (72/97) to saccades.

Fixation cells

Fixation cells (25/97) discharged after saccades and continued to discharge for the entire period of fixation. In twenty-three cells, the spontaneous activity was very low (from 1 to 4 spikes/s), while in the other two cells, the spontaneous activity ranged from 10 to 25 spikes/s. The rate of discharge during fixation varied, from cell to cell, with a maximum of 70 spikes/s and a minimum of 0 spikes/s. None of these neurons showed an increase in discharge before saccades. The discharge started at the end of the saccades.

The delay varied from cell to cell and among the trials, ranging from zero to 300 ms. We studied the delay in fifteen cells for ten trials each and found that the discharge started immediately after the saccade (0–40 ms) in 60% of the trials randomly selected (Fig. 3).

These units were involved with fixation and not merely position since the neurons were not active when the monkey returned its eyes to the same position without performing the task in rest conditions (Fig. 4A and B). Each of these cells was tested with classic visual stimuli (bars, dots) and with complex, motivational stimuli (colored objects and pieces of fruit).

We did not detect a visual receptive field for any cell. The possibility of a very small foveal receptive field was discarded because the cells discharged when the monkey maintained active fixation in the absence of a fixation point. For example, the cell discharged when the monkey both pressed the bar during the intertrial period and looked at the position of the unilluminated fixation point in total darkness (Fig. 5A and B). This indirect test was accomplished from four to sixteen times for each cell.

These cells did not show a visual receptive field nor any coding of orbital position. Consequently, we used the term fixation field to refer to the spatial location delimited by active or inhibitory responses during fixation. Of all the cells, 12 showed a very small central fixation field as shown in Figs. 6 and 10. The other

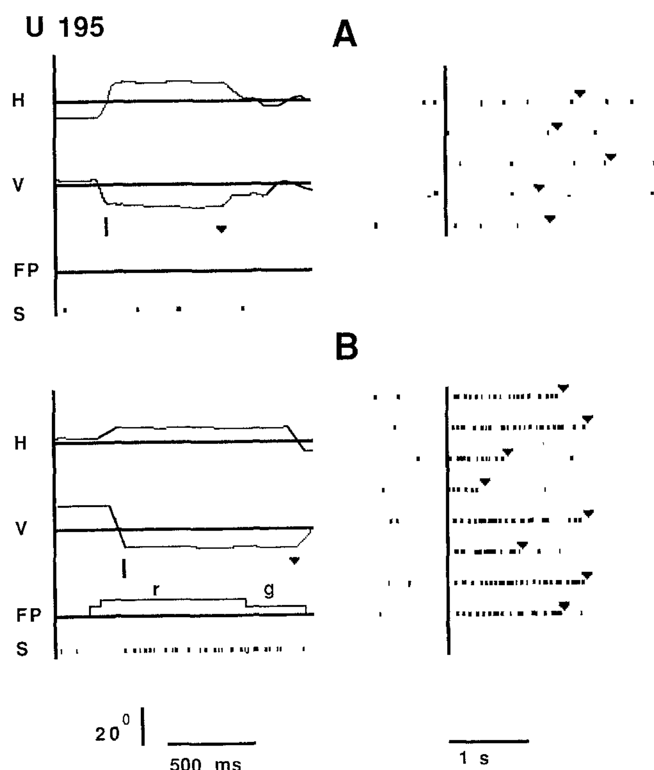

Fig. 5A, B. An example of cell discharge during the intertrial period **A** and fixation task **B** for the same eye position. In **A**, the animal pressed the bar during the intertrial period and the LED was off. In **B** the monkey made a correct response and the LED was on. In both situations, the eye was at the same position and the attention was engaged. This comparison allowed us to discard the possibility of a small receptive field. H: horizontal component of the eye position; V: vertical component of the eye position; B: bar signal; r: red period; g: green period; S: spikes; each dot represents one spike. The rasters are synchronized with the onset of fixation. The triangles represent the end of the fixation

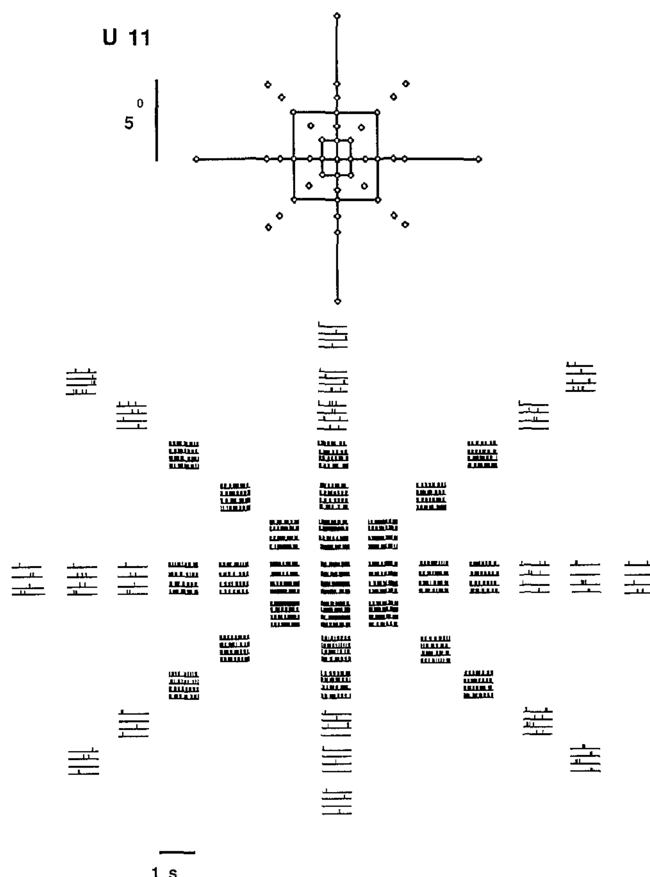

Fig. 6. Fixation field. This cell discharged when the animal made a fixation at the central position in the head coordinates. Upper: the diagram represents the tested positions (dots); the lines connect the points with the same frequency discharge. The mean frequency was 45.4 sp/s (± 10.3 sp/s) in the center of the fixation field and 30.5 sp/s (± 5.1 sp/s) around it. Lower: rasters show the discharge at each location represented above. Each line represents a trial. When we found a fixation neuron, we tested first with an array of 25 LEDs, and then we moved the LEDs to other parts of the visual field in order to achieve a definition of the field

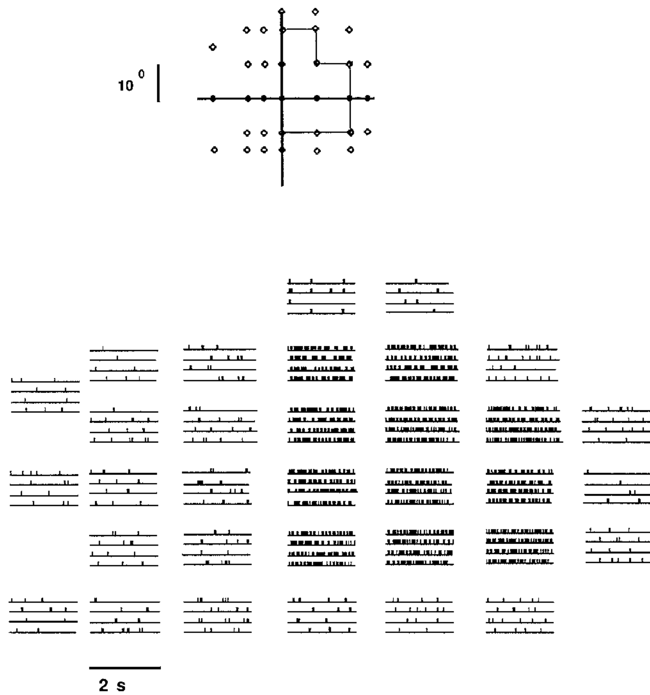

Fig. 7. Fixation field. This cell showed a contralateral fixation field. The mean frequency of discharge was 25.6 sp/s (± 10.5 sp/s)

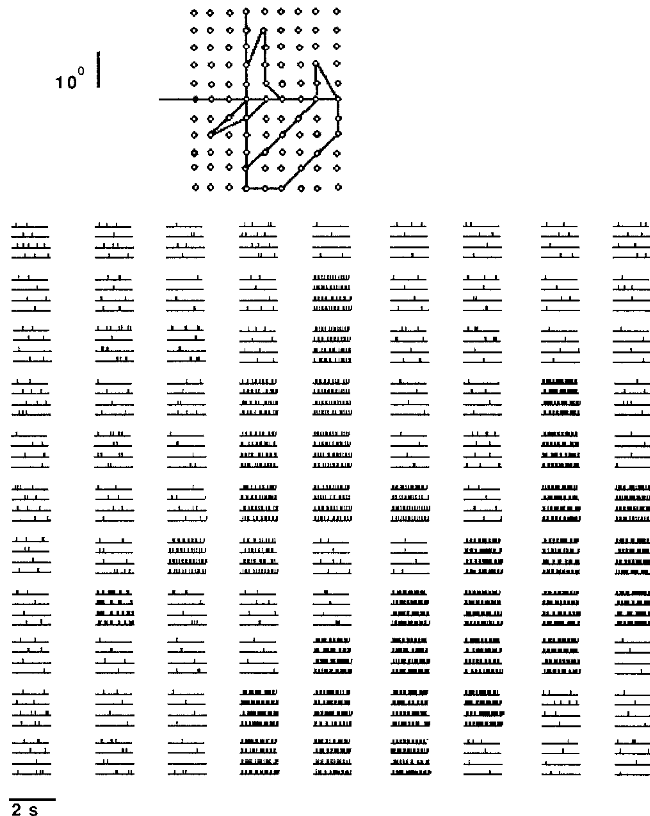

Fig. 8. Fixation field. This fixation neuron showed a double field which was predominantly contralateral. The medial field showed a mean frequency of 10.4 sp/s (± 3.1 sp/s); the lateral field showed a mean frequency of 20.4 sp/s (± 2.1 sp/s)

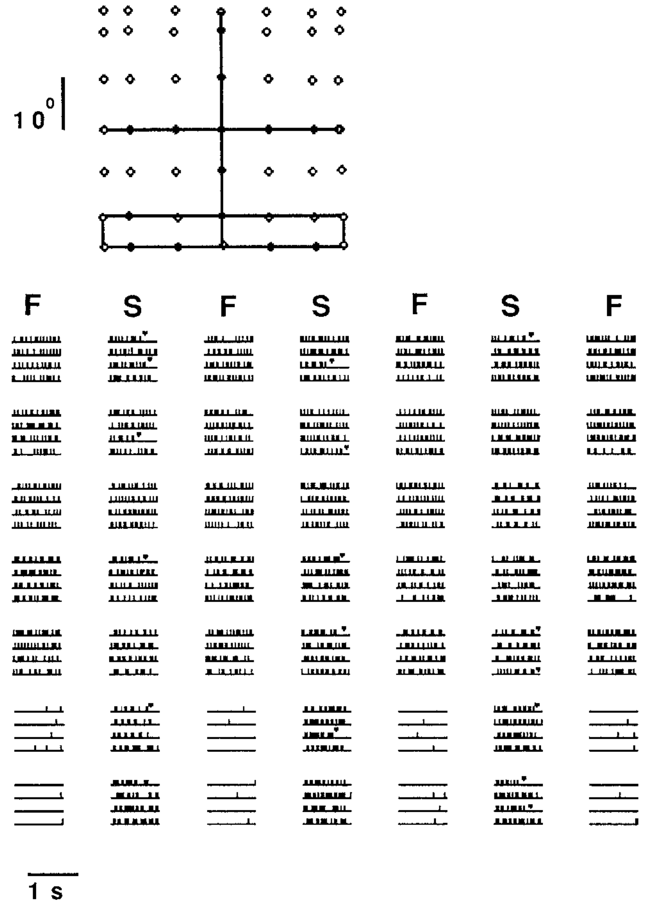

Fig. 9. Inhibitory fixation field. This fixation neuron showed the same frequency of discharge during fixation (F) and during spontaneous gazing (S) outside of the task. The discharge stopped when the animal made a fixation at 20 or 25 deg down. In the raster representation, we alternate fixation (F) and spontaneous gazing (S) to show that differences were present between 20 and 25 deg in the lowest part of the tested visual field during fixation. The mean frequency of discharge in the inhibitory field was of 1 sp/sec (± 1). Each raster represents a target location and the triangles represent the end of free gazing

neurons presented different fixation fields that were predominantly contralateral.

Twenty-three neurons were excitatory. During the fixation period their discharge increased in some visual field locations (Figs. 7, 8 and 10). Two cells showed an inhibitory response. These two cells were characterized by a spontaneous discharge that was inhibited during fixation. One of these cells had an inhibitory fixation field between 20 and 25 deg in the left part of the visual field; the other neuron had an inhibitory between 20 and 25 deg in the lower part of the visual field (U 28 Figs. 9 and 10).

The electrical stimulation (30–50 μA) at the site of the fixation neurons drove the eye to the orbital position associated with the activity of the cells (Fig. 11A). This effect was tested in seven neurons with a contralateral field and in the two cells that showed an inhibition of the spontaneous discharge during fixation (Fig. 11B).

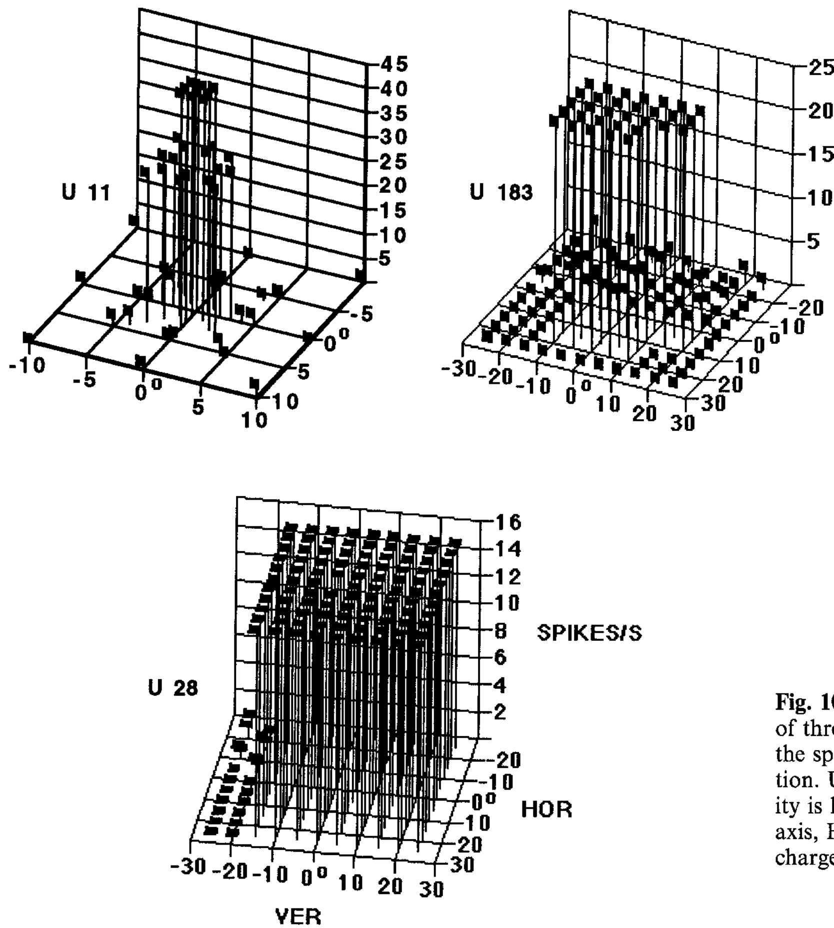

Fig. 10. Three dimensional representation of fixation fields of three units. U11 and U183 excitatory fixation fields: the spontaneous activity is low and increases during fixation. U28 inhibitory fixation field: the spontaneous activity is high and is inhibited during fixation. Ver: vertical axis, Hor: horizontal axis; Freq: mean frequency of discharge (spikes/s)

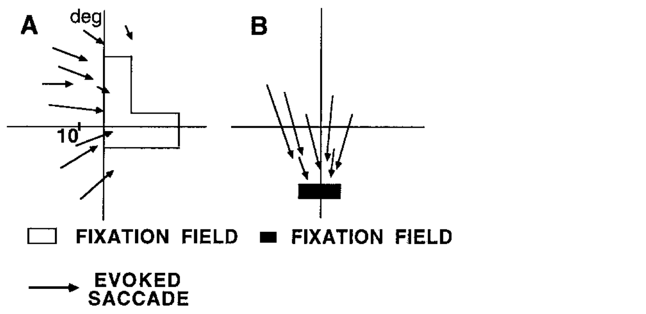

Fig. 11A, B. Two-dimensional representation of fixation field with the trajectories of electrically evoked saccades overprinted. **A** excitatory field; **B** inhibitory field. We stimulated also when the eyes were in other positions (A: right, B: left and right) but we did not evoke saccades

These cells may also be involved in three other functions: 1) vergence, 3) post-saccadic activity for saccades with a preferred direction, 2) head orientation. The possibility that vergence was involved was very low, however, because all the stimuli were at the same distance from the animal (2 m). We did not explicitly test to see whether these cells were postsaccadic cells for saccades with a preferred direction, but we did not see activity after equivalent orienting saccades during the fixation task. We could not test to see if head orientation was involved, but increases of EMG activity were not observed during the fixation period. Further investigation is needed to determine whether a detailed spatial map exists.

Saccade cells

Cells which discharged before saccades were divided into the following categories:

Visually guided and spontaneous	6/72
Visually guided	6/72
Checking	27/72
Checking and spontaneous	8/72
Spontaneous	15/72
Novelty detection	10/72

We applied the term checking-saccade cells (27/72) to the phasic neurons that discharged only when the monkey made the saccade toward the "off" LED (Fig. 12 CS) during a 2 LEDs task; this effect occurred in both light and dark conditions. These cells either were not active for visually guided saccades toward the same "on" or gave only one or two spikes (Fig. 12 VGS). The neural activity was independent of the eye movement's direction and amplitude, and of the visual stimulus (Fig. 12 V).

Of all these cells, two presented bursts of activity with a mean frequency of 49.8 spikes/s (± 10.2 sp/s) (Fig. 12 U46). These cells also showed spontaneous activity.

The other 25 cells were characterized by bursts with a low mean frequency of 20.3 spikes/s (± 5.7 sp/s)

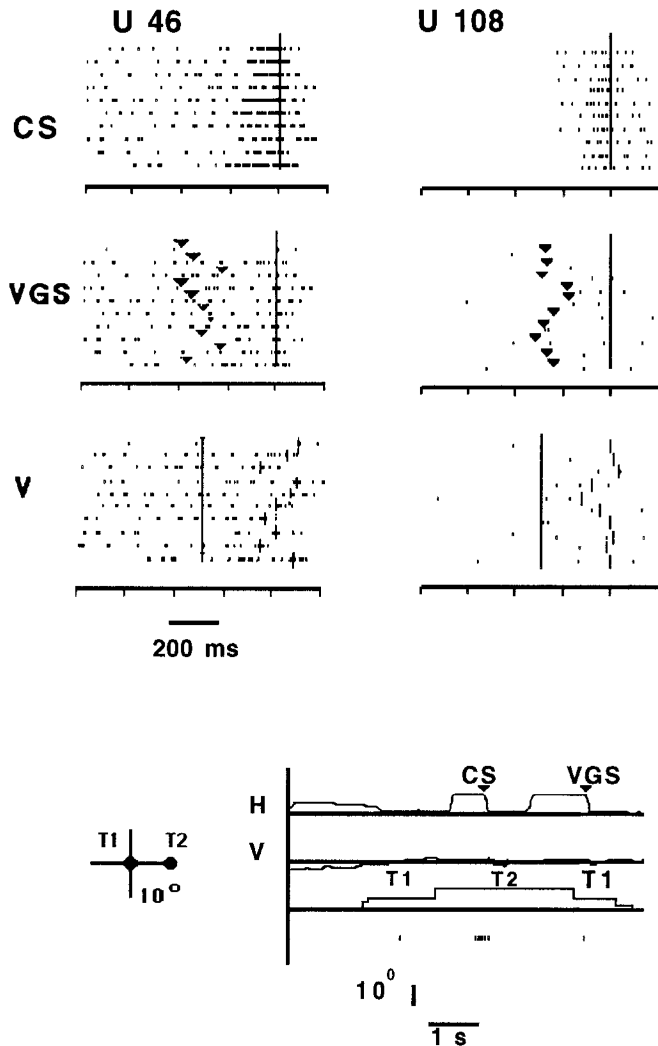

Fig. 12. Checking saccade neuron. Lower diagram. The animal made a checking saccade (CS) from the "on" target T2 to the "off" target T1. The animal made a visually guided saccade from T1 toward T2 and from T2 toward T1. H: horizontal component of the eye movement; V: vertical component of the eye movement; T1: central target; T2: peripheral target; S: spikes; each dot represents one spike. U46 is one of the two cells with a high frequency. U108 is a classic checking saccade unit at low frequency. CS: raster synchronized with the onset of checking saccades; VGS: raster synchronized with the onset of visually guided saccades; V: raster synchronized with the onset of the visual stimulus

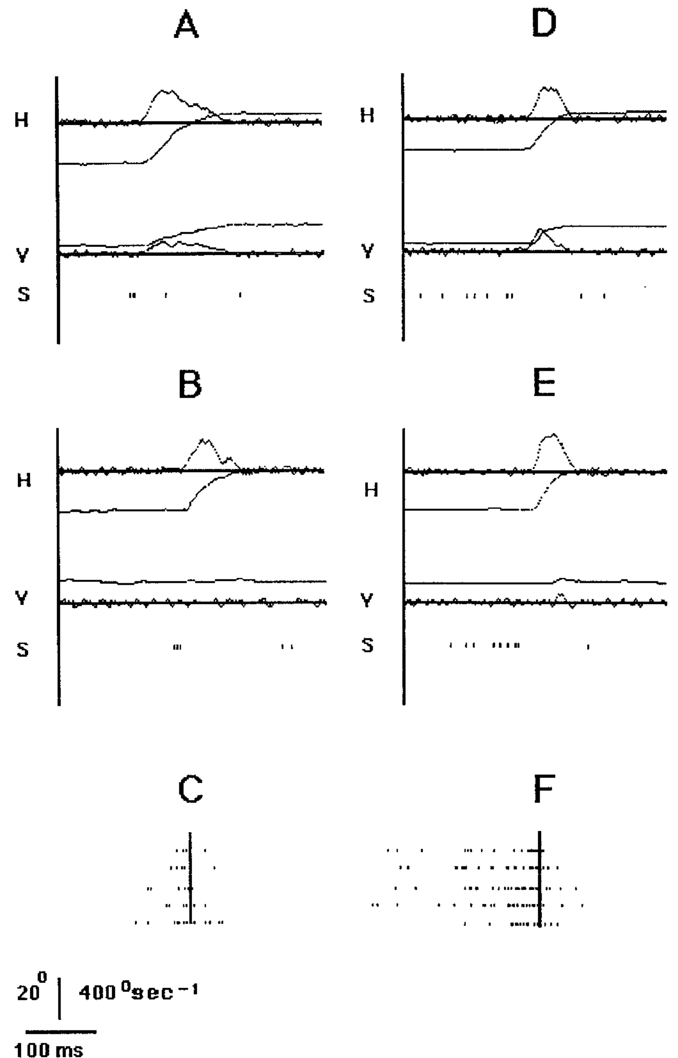

Fig. 13A–F. Spontaneous saccade cell in dark. **A–C** Show the cell's discharge before irregular saccades. **D–F** Show the cell's discharge before regular saccades. In **C** and **F**, the rasters are computed for saccades with similar static and dynamic characteristics. H, V: horizontal and vertical component of eye movement and istantaneous velocity. S: spikes

(Fig. 12 U108); in these cells spontaneous activity was nearly absent.

The cells were almost completely silent between checking saccades; the discharge started 100–260 ms before the onset of a saccade. In all cells, the discharge stopped 100–200 ms after the end of a saccade.

Eight cells also discharged for some spontaneous saccades that occurred outside of the task. We were not able to define the relationship between discharges and saccades because it was erratic and not related to the static or dynamic parameters of the saccades.

Spontaneous eye movement cells showed a phasic discharge before the onset of a saccade. We found that the activity of eleven of these cells was related to the velocity profiles of the saccades.

The discharge was weak or completely absent when the velocity profile was characterized by multiple velocity maxima or inflection points (irregular saccades) (Fig. 13A, B and C). By contrast, the discharge was brisk when the velocity profiles showed single velocity maxima (regular saccades) (Fig. 13D, E and F). In addition, the onset of the saccades occurred less than 100 ms before the irregular saccades but about 200 ms before the regular ones. We compared saccades with similar characteristics (direction, amplitude and velocity), to be sure that parametric differences were not involved.

Ten percent of cells (10/97) discharged upon presentation of new stimuli. Of these ten cells seven were active only during the first of a series of trials. The discharge was not always present when the monkey made saccades in response to complex figures and objects. The discharge was also inconsistent when the experimenter stood in front of the animal. The saccades showed similar parametric characteristics (velocity, direction and amplitude).

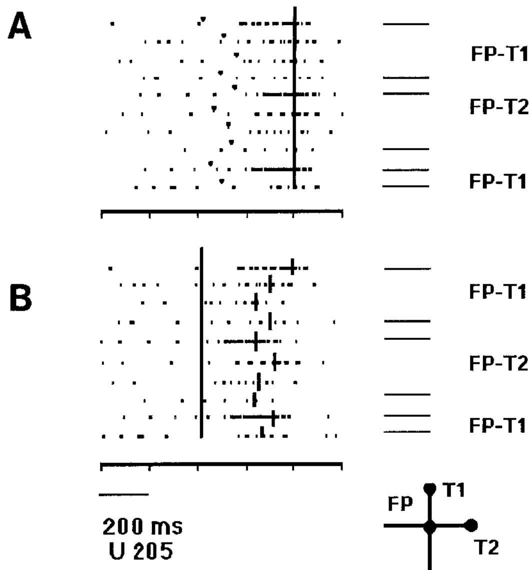

Fig. 14A, B. Novelty detection neuron. **A** raster synchronized with the onset of saccades; **B** raster synchronized with the visual stimulus. FP–T1 represents the discharges for saccades from the fixation point (FP) to target T1; FP–T2 represents the discharge for saccades from the fixation point to target T2. In the raster, the discharges are arranged in chronological sequence

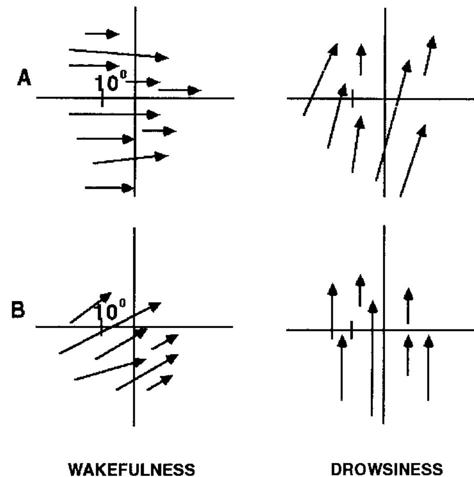

Fig. 15A, B. Two cases of rotation of fixed vector saccades. In **A** the electrically evoked saccades are horizontal during wakefulness and became predominantly oblique and vertical oriented during drowsiness. In **B**, the electrically evoked saccades were oblique during wakefulness and became vertical during drowsiness. Vertically oriented eye movements were rapid eye movements and not slow drifts

Generally, the firing was brisk at the beginning and became weaker as the trials progressed.

Seven of these saccade cells showed habituation during the saccade task. In the task, three LEDs were present: a central fixation point (FP), a target (T1) on the vertical axis, and a second target (T2) on the horizontal axis (see Fig. 14). In the first trial, the discharge was intense, decreasing in successive trials (Fig. 14A–T1). If the animal made a guided saccade toward a second target, the discharge was strong at first and then habituated again (Fig. 14A–T2). If the first target was switched on after some trials, the discharge became brisk again (Fig. 14A–T1).

Electrical stimulation

In the experiments of Schlag and Schlag-Rey (1987a, b) as in ours, electrical stimulation evoked end-point and fixed-vector eye movements. In addition, the stimulation modified the trajectory in the fixed-vector direction during spontaneous saccades.

In the present study the direction of the fixed vector was modified by the arousal level, shifting from a horizontal to a vertical orientation when the animal became drowsy (Fig. 15). This finding was verified in both animals. But the changes of behavioral state were present only in two locations, one for each animal. The movements evoked by electrical stimulation were rapid and did not resemble the vertical shift of synchronized sleep (Berlucchi et al. 1964; Bon et al. 1980). In some penetrations, the electrical stimulation had no effect even if the neurons were saccade related. In these cases, we used an intensity of current up 150 μA.

In addition, we tested to see whether in this area attentive fixation modified the electrical threshold necessary to evoke saccades. When the animal made a fixation, doubling the intensity of current (80–100 μA) was necessary to evoke a saccade. The evoked saccades maintained the same direction as those that occurred during spontaneous gaze, but the amplitude was about half as great. At some cortical points, it was impossible to evoke saccades during fixation, even using currents up to 150 μA.

Discussion

Most experiments in this area have been carried out on trained rather than on untrained monkeys. With trained animals it has been possible to study motor behavior accurately in relation to given instructions. On the other hand, it is also possible that the animal's behavior is more physiological in spontaneous monkeys; thus the activity of the neurons may represent the real activity of the cells. In trained monkeys, the recordings may be influenced by cognitive and motivational processes. In an attempt to investigate this issue in a more natural condition, we trained monkeys for fixation and saccade tasks in an unstressful condition. They were free to work at will, and they were used to interacting with the experimenters during the tasks as well as at other times. Our animals performed the saccade task many times with a saccade reaction time longer than that reported by other authors.

Fixation neurons

Our fixation neurons encode the active fixation of the eye in space. These neurons do not however encode eye position per se and are not directly involved in visual

processes. Two previous papers described neurons with some features similar to ours but at a prefrontal level. The Type II cells studied by Bizzi (1968) discharged when the animal's eyes were oriented in a specific direction and during smooth pursuit movements; these cells were not active before saccades. Suzuki and Azuma (1977) found neurons activated by attentive gazing to all positions in the visual field. Both reports showed that light has little influence on discharge activity. Bizzi proposed that the type II cells might be involved in complex coordination, such as eye-head-limb movements. Suzuki and Azuma postulated that the function of gaze neurons was to maintain the attention of the animal to a specific visual stimulus.

Three principal issues are of interest about the fixation neurons we have described here: 1) they have a field of fixation, and the discharge is only active after the saccades and finishes at the end of fixation; 2) for the tested neurons the fixation field represented the end-point for electrically evoked saccades; 3) the fixation neurons are intermingled with saccade cells. With these data it is not easy to make inferences about the electrically evoked saccades toward the fixation field, but we will speculate about a possible mechanism. The most reliable inference is that fixation neurons are clustered with saccade neurons. When we stimulated the fixation neurons electrically, we may have activated antidromically saccade neurons that produced saccades toward the fixation field.

Goldberg and Bruce (1990) studied the frontal eye field cells under the double-step paradigm and postulated that the critical signal from the frontal eye field is neither the retinal location of a saccade target, nor its spatial location, but rather the saccadic movement that the target evokes. In their model, the dimensions of the second saccade is calculated by vector subtraction of the dimensions of the first saccade from the vector described by retinal location of the target. They suggested that the subtraction may be performed by postsaccadic neurons in the frontal eye field. We propose that the subtraction might be performed also at dorsomedial frontal cortex level.

We have developed two further hypotheses concerning the role played by fixation neurons. First, the neural activity may influence the discharge of visual neurons of the posterior parietal cortex. Mountcastle et al. (1981) found that many of these visual neurons show changes in the intensity of their discharges during attentive fixation. This hypothesis is sustained by anatomical evidence (Goldman-Rakic 1988) that shows a strong connection between the frontal lobe and the parietal cortex.

Second, the neurons may play a role in complex mechanisms involved in the selection of motor strategies for such behaviors: catching visual targets with the sight or reaching an intended position in space with the arm. This second possibility is supported by studies of cortical lesions and by neuropsychological and electrophysiological evidence. Humans with a lesion in the frontal cortex cannot refrain from making a saccade in response to a visual stimulus (Guitton et al. 1982). Neuropsychological investigations suggest that the frontal lobe is active in situations involving the detection of events (Posner and Petersen 1990) and in targeting processes of selective attention (Posner and Rothbart 1991). Rizzolatti et al. (1990) described neurons in the rostral part of area 6 which were involved in arm movements. They proposed that this area plays a role in the preparation of reaching-grasping arm movements. We (Bon and Lucchetti 1991) found cells at a dorsomedial frontal cortex level that showed a double-firing discharge: the first burst occurred before the arm movement and the second before related eye movement. We proposed that arm-eye cells related to a purposeful movement may be attributed to a motor reactivation or an ordering signal.

Saccade neurons

The checking saccades closely recall the "spontaneous saccades" observed by Schlag and Schlag-Rey (1987a). In their experimental situation, the animal did not know the position of the target, while in our paradigm (2 LED), the monkey knew the target position. The neural activity of the checking saccade cells did not codify the saccade parameters; the activity may be considered an activation command for self-initiated saccades, which we call voluntary saccades. Bruce and Goldberg (1985) hypothesized that the frontal eye fields are the cortical area for voluntary saccades. Then, it is possible that voluntary eye movements are under the control of two areas: the dorsomedial frontal cortex and the frontal eye fields. The electrophysiological evidence is sustained by anatomical investigations. In fact, frontal eye fields and supplementary eye fields project to the same premotor structures (superior colliculus and pontine structures) as shown by Shook et al. (1991). Kurata and Wise (1988) made comparable observations for self placed arm movements in the supplementary motor area and in the premotor cortex.

Regarding the two different patterns of discharge in spontaneous eye movements, we believe that a different level of activation is present. Anatomical evidence (Shook et al. 1990; Huerta and Kaas 1990) suggest that there are direct projections from this area to the pontine structures involved in the control of eye movement. One possibility is that a different intensity of firing at the frontal level programs the saccade with a different temporal pattern. The reduced activation during the trials of the novelty detection neurons might be an expression of reduced attention as well as of a short spatial memory process.

Conclusions

Our results provide insight into two issues. First of all, they confirm our previous hypothesis that the dorsomedial frontal cortex is involved in fixation (Bon and Lucchetti 1990). We propose that these fixation neurons may be involved in encoding the saccade toward a target. They could play a role in arm-eye-head motor-planning primarily in the targeting the goal of the movement.

Secondly, the fact that neurons discharge for self-initiated saccades implies that this area may share the control of the voluntary saccades with the frontal eye fields. This neural activity implies that activation is involved in intentional motor processes.

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