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The Discharge Characteristics of Single Units in the Oculomotor and Abducens Nuclei of the Unanesthetized Monkey

PETER H. SCHILLER

Department of Psychology, Massachusetts Institute of Technology
Cambridge, Massachusetts (USA)

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Summary. 1. Extracellular single unit records were obtained in the brainstem oculomotor complex of alert monkeys.

2. Maintained eye position, smooth pursuit and saccadic eye movement appear to be brought about by the same population of neurons.

3. Increasing deviation in eye position for fixation and for smooth pursuit movement is accomplished in two ways: (a) increase and decrease in firing rate and (b) change in the number of neurons discharging concurrently.

4. Saccadic eye movement is brought about by a rapid burst of firing in these same units. Saccade size is determined by the duration of the burst; the speed of the saccade appears to be influenced both by discharge frequency and the size of the neuronal pool discharging in synchrony.

5. A small population of units discharges specifically in association with vergence operations, increasing their firing rate to convergence and decreasing it to divergence.

Key Words: Oculomotor system — Eye movement control — Abducens nucleus Brainstem

Introduction

Single unit activity in the brainstem oculomotor complex has been recorded in several species, particularly during nystagmus (Azzena, 1966; Bertrand, Minini and Tyč-Dumont, 1966; Dumont-Tyč and Dell, 1961; Horcholle-Bossavit and Tyč-Dumont, 1969; Lorente de Nó, 1953; Manni, Casey and Dow, 1965; Precht, Richter and Grippo, 1969). Until recently however, these studies have been restricted to animals that were under anesthesia or which had sustained transection of the neuraxis at various levels. Yet it is known that the eye movements one encounters in the behaving organism are for the most part absent under such experimental conditions. For this reason little is known about the discharge patterns of single neurons in the oculomotor complex that appear during normal eye movements.

Behavioral studies have defined several classes of eye movement, the distinct characteristics of which led some investigators to suggest that different neural mechanisms are responsible for them (Dodge, 1903; Dodge, Travis and Fox, 1930; Rashbass and Westheimer, 1961; Young and Stark, 1963). It has been proposed that there are at least four different systems, giving rise to saccadic eye

movement, smooth pursuit eye movement, vergence operations and the vestibular control of eye movement (Robinson, 1968).

In order to better understand the neural control of oculomotor activity, investigators in a number of laboratories have begun to record the action potentials of single neurons in the alert, behaving animal in those brain structures which are implicated in oculomotor control. The techniques developed by Evarts (1966) for recording in this fashion from the rhesus monkey are particularly well suited for the investigation of eye movement, since the oculomotor system of the monkey is highly developed and the characteristics of simian eye movements, which have been studied on the behavioral level by Fuchs (1967), are in many respects quite similar to those in man.

The activity of single units in the frontal eye fields of the awake rhesus monkey has already been subjected to study by Bizzi (1968) and Bizzi and Schiller (1970). The findings suggested that there are at least two different classes of neurons in this area: those which discharge in association with saccades and those which exhibit maintained firing in relation to eye position in the orbit. Most of the neurons studied so far did not discharge prior to eye movement, drawing into question the contention that the frontal eye fields are involved in the initiation of eye movement (Adler, 1965). The presence of the two different classes of neurons, however, is consistent with the view that different neural systems are involved in the control of the various kinds of movement, at least at this particular level of the oculomotor system.

Interpretation of these findings is difficult unless one offers comparable information on the activity in other structures related to eye movement control. In order to gain this information for neurons which comprise the final common path to the extraocular muscles, extracellular records were gathered from single units in brainstem oculomotor and abducens nuclei of alert, behaving monkeys.

Method

Recordings from the oculomotor nucleus were obtained in four rhesus monkeys weighing 6—8 lbs. In one of these animals units were also recorded from the abducens nucleus.

Each animal underwent two aseptic surgical procedures. During the first four, screws were implanted into the skull under nembutal anesthesia, using a technique similar to that described by Evarts (1966). These screws were subsequently used to immobilize the animal's head during the recording sessions.

The second operation was done approximately one month after the first in three steps: 1) implanting of a 21 gauge stainless steel tube terminating above the oculomotor nucleus (and abducens in one monkey) through which the microelectrodes were subsequently lowered; 2) implanting of silver-silver chloride electrodes for eye movement recordings; and 3) placement of gross electrodes in two monkeys for antidromic stimulation of the third nerve. Recordings began typically 1—2 weeks after this operation.

1. Restraining Method

After the second operation, monkeys were placed into a primate chair. During the recording sessions the head of the monkey was secured to a headholder by means of the implanted skull screws in a manner similar to that previously described by Bizzi and Schiller (1969).

2. Unit Recordings

The single unit records in this study were obtained using 9 mil tungsten wire coated with Isonel 31, as described by Marg (1964). These electrodes were inserted through the implanted 21 gauge tube. The tube was placed 8—11 mm above the oculomotor nucleus at A 3—4 mm,

L 3—4 mm, using a 20° angle in the coronal plane to minimize damage to midline structures. The upper part of the tube passed through a small plastic piece (Delrin) which was fixed to the skull with dental cement. The microdrive was secured to the plastic piece on which it could be rotated 360°. To facilitate the lowering of the microelectrode, a 4 mm section of the upper end of the 21G tube was filed down halfway across its axis. Thus, the electrode shaft was first placed against the exposed inner wall of the tube and then lowered. Electrodes were manually advanced to a point just approaching the tip of the tube in the brain and were thereafter advanced with a hydraulic microdrive made up with two tuberculin syringes. The syringe of the head stage was cut down in size and was housed in an aluminum holder designed to allow 360° rotation. The other end of the microdrive consisted of a syringe coupled to a micrometer. This method was developed after considerable experimentation and proved to be better for our purposes than available commercial products. Variation in electrode placement was achieved by bending the electrodes. Such curved electrodes described an arc as they emerged from the tube. Because of the relatively sharp taper of these electrodes (Marg, 1964), their tip did not scrape against the walls of the tube. By varying the degrees of curvature and the rotation of the drive, an area of 2—3 mm could be systematically explored. Changing a pass could be accomplished simply by withdrawing the electrode into the tube, rotating the microdrive and advancing the electrode once again. A record was kept of the degree of bend and rotation for each pass as well as the depth of the recording site. Electrodes were selected using the method of Bak (1967). We have found that electrodes between 4 and 10 pF provided the best results in our recordings.

During the last day of recording, electrolytic lesions were placed at the end of the electrode tracks made on that day. Histology was performed on each brain by staining every 25 μ section through the oculomotor and abducens nuclei with cresyl violet. Because of the sharp electrode taper, the majority of the tracks could be visualized.

The extracellular action potentials were amplified using a FET circuit (Wall, Freeman and Major, 1968) and a Grass AC preamplifier. The data were recorded on a Honeywell 8100 FM tape recorder along with the eye movement record, voice, and a marker channel. The signals for on-line observation were displayed on 565 and 503 Tektronix oscilloscopes and a loudspeaker for unit activity.

3. Eye Movement Recording

After surveying various methods of eye movement recording, the electrooculogram (EOG) was chosen. To record the EOGs we employed silver-silver chloride electrodes (In Vivo Metric Systems — Porous Ag/AgCl pellets, size C). These electrodes were recessed 1—1$^1/_2$ mm in a nylon cup having a small lip. The electrodes were implanted around the orbit, one each above and below the eye for vertical recording, and two on the temporal bone of each eye for horizontal recording. The nylon cup was secured to bone with a No. 80 stainless steel screw going through a small hole in the lip of the nylon cup. Prior to implantation, a drop of 2% agar in distilled water was placed on each electrode in the cup, thus providing a 1 to 1—1$^1/_2$ mm thick agar bridge between it and tissue. The leads of the electrodes were then brought out to a Sheatz pedestal secured to the monkey's skull.

Within about a week after implantation these electrodes produce records which are quite stable. Provided that the agar bridge is not damaged during surgery, they are far superior to surface EOG electrodes and will record well for several months. In most of our recordings we used Hewlett Packard 8300 chopper stabilized DC amplifiers, which have no measurable drift under these recording conditions. As an added precaution we calibrated eye position for straight — ahead gaze for the majority of units studied. For the calibration procedure we employed a black perimeter, having an edge diameter of 31 in. and a radius curvature of 18 in. which was placed in front of the monkey 18 in. from the eyes. The perimeter had $^3/_4$° holes drilled every 10° in the horizontal and vertical planes and at 45° diagonals. Each of these holes was covered with a black rubber stopper. Removing a stopper and peeping through the hole or wiggling a finger causes the monkey to look at the opening. A marker was used to indicate on the tape record when the monkey was looking at each of several selected holes. For these calibrations, the eye movements, marker, and the experimenter's voice, were recorded on tape. In addition, to obtain zero offset and accurate voltage values, we used a dual slope digital voltmeter (Fairchild, Model 7050).

With this calibration method, we found that the voltage output from the eye movement electrodes was reasonably linear over a range of about 60°. Any deviation from this could be corrected by the calibration procedure.

In two of the four monkeys gross electrodes were implanted during the second operation to permit antidromic stimulation of the third nerve. However, due to the proximity of recording and stimulation sites, the stimulus artifact proved to be too large in most cases for adequate identification of units.

4. Data Collection Procedure

Recordings from each monkey were undertaken over a period of 2—4 weeks. During the experimental sessions, the activity of each unit was recorded on magnetic tape for 10—25 min along with eye movements, voice and calibration; some units were lost before recording was completed. The majority, however, could be held for extended periods. During some parts of the recording session eye movements were spontaneous; during others, various objects of interest were moved in front of the monkey in order to obtain records of pursuit movement and a large number of eye positions. Since the monkeys were continuously shifting their gaze, we encountered no difficulties in obtaining active eye movements. Units were also studied in conjunction with vergence movements. This was accomplished in two ways: (a) objects of interest to the monkey were moved toward and away from the animal while observing the position of the eyes. A marker and voice were recorded on magnetic tape concurrently with eye movement and unit activity. (b) Two 10° prisms were placed in front of the monkey's eyes which forced the animal to converge excessively in order to bring visual stimuli on the same part of each retina.

5. Data Analysis

The data were analysed first by displaying the recorded information on the oscilloscope and loudspeaker. Satisfactory records were then photographed on 35 mm film using a Grass camera. Quantitative analysis was carried out by counting unit discharges relative to eye movement as displayed on these photographs. Such analyses were carried out for eye position, saccade and pursuit activity.

Results

The activity of 190 units was recorded on magnetic tape. Subsequent analysis reduced this number to 139 clearly isolated single units in the oculomotor complex. The gross distribution obtained is shown in Table 1. The specifications in this table refer to the conditions under which a given set of units increase their firing rate. For directionally specific units this will be called the "ON" direction.

Table

Directionally Specific Units		Other Relations	
Deviation up	37	Convergence	7
Deviation down	18	Eye lid	2
Deviation to the left	7	Multiple directions	10
Deviation to the right	56	Inhibition during saccade	2

Three basic criteria were used in identifying single units related to the motor control of eye movement: (1) clear relationship between the eye movement records and unit discharge; (2) onset of neuronal activity occurring prior to initiation of saccadic eye movement; and (3) histologically established location of passes in the oculomotor and abducens nuclei. Because antidromic stimulation was unsuccessful, we were unable to unequivocally identify motor units. Thus it is possible that some portion of the units we recorded from were either interneurons or fibers. The probability of recording from interneurons would seem

rather low as Warwick (1964) has shown that practically all neurons degenerate in the oculomotor nucleus after the oculomotor nerve has been severed. On the other hand, it was not possible to make a clear distinction between fibers and cells, especially since the wave form of the signal was similar for both. Some of the guidelines we used were the following: small amplitude signals, inability to isolate single units with a good electrode, rapid appearance and disappearance of the signal upon advancing the microelectrode and failure to kill the unit was believed to implicate fibers. The opposite criteria, particularly the maintenance of the signal over many micra and the subsequent killing of a unit, led us to judge the recording to have been from a cell.

1. Directionally Specific Units

The characteristics of a typical neuron in the oculomotor nucleus increasing its firing rate to downward eye movement is shown in Fig. 1. Two sets of traces are shown, one associated with primarily saccadic and positional activity and one with smooth pursuit activity. The upper trace gives the unit discharge and the lower, the vertical eye movement record. The horizontal lines in the eye movement record represent vertical displacement of eyes in degrees deviation from straight — ahead gaze. The following points should be noted: (a) The rate of discharge is proportional to eye position, with frequency increasing as a function of downward deviation of the eye. (b) A burst of firing occurs prior to and during downward saccades; a corresponding inhibition is seen with upward saccades. (c) A burst of firing occurs for a downward saccade even when the ensuing eye position is one where the unit does not sustain its firing (see extreme right part of upper trace). (d) Firing does not commence during tracking until the eye is near straight — ahead gaze (0°).

The type of activity noted in a, b, and c is characteristic of almost all of the units recorded in the oculomotor and abducens nuclei, suggesting that at this level saccades and smooth pursuit are brought about by the same set of neurons.

Fig. 2 shows the discharge characteristics of two neurons in the right abducens nucleus innervating the right lateral rectus muscle. The two units shown were obtained in succession in the same pass and were less than 200 μ apart. Both units increase their firing in association with eye movement to the right. Unit W-6-3 does not shown any sustained activity until the eye deviates abot 20° to the right. By contrast, unit W-6-4 shows maintained activity when the eye is still in a position deviating 20° to the left. This suggests that for eye position or pursuit movement neurons initiate their tonic activity at different degrees of eye deviation.

In order to verify and extend the observations noted so far the data were analyzed quantitatively. Unit discharge characteristics were assessed with respect to both eye position and saccadic eye movement.

a) Quantitative Analyses of Unit Discharge Associated with Eye Position

Measurements of unit activity in relation to eye position were obtained by counting the spike potentials on the photographed records. Counts were typically taken for 100 msec time samples for each eye position not including the bursts at saccades or pursuit movement.

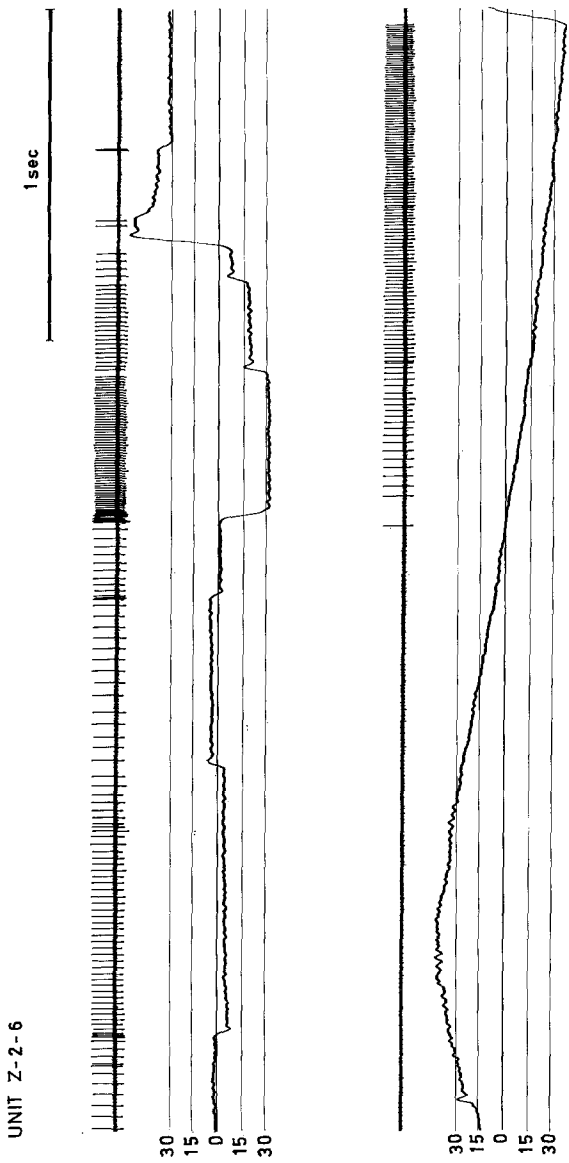

Fig. 1. *The extracellular discharge characteristics of a single cell in the oculomotor nucleus increasing its firing rate in association with downward eye movement.* Upper trace is the unit and the lower, the vertical eye movement. The horizontal lines with the eye movement record represent coordinates in degrees of deviation from straight ahead gaze; upward deflection corresponds to elevation and downward deflection to depression of eye. The upper set of traces represents spontaneous saccadic eye movement with intervening periods of fixation. The lower set of traces shows unit activity during smooth pursuit brought about by moving an object in front of the monkey

Figure 3 shows the discharge frequency of four units in the abducens nucleus. These units were selected to highlight several points regarding rates of firing for maintained fixation. This figure demonstrates that, (a) firing frequency, when plotted against eye deviation in degrees, yields a linear function. The majority of the units plotted in this fashion gave a linear relation between firing rate and eye deviation. (b) The onset of firing of each unit is observed at different degrees of eye deviation. (c) The rate of increase in firing varies considerably from unit to unit.

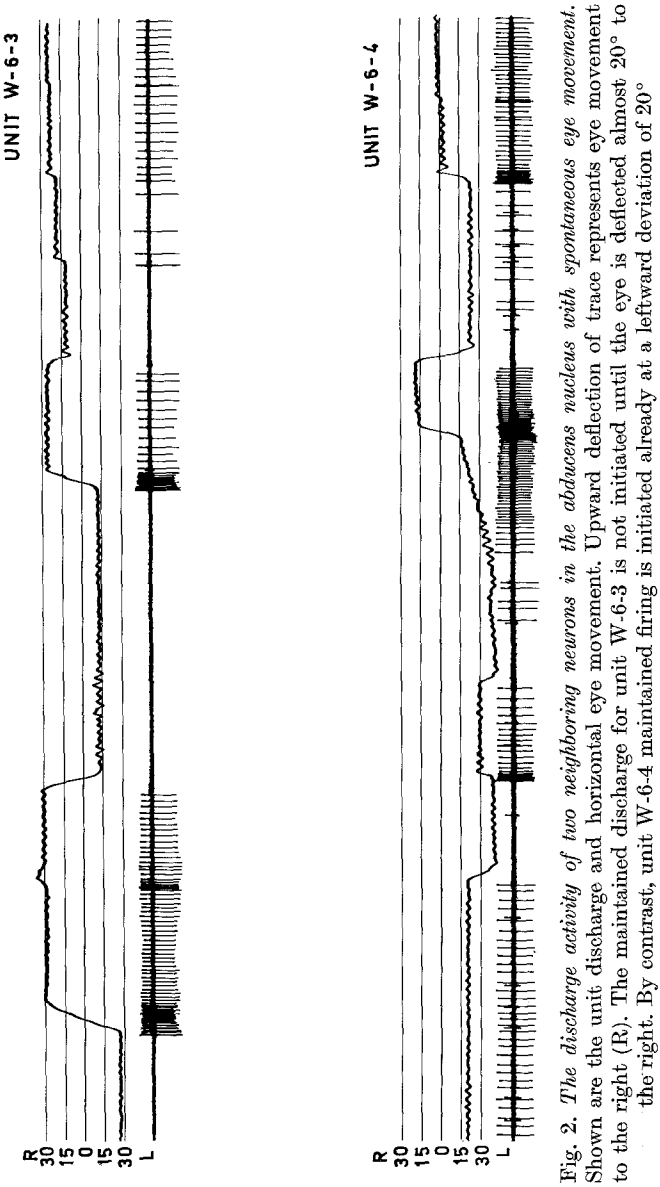

Fig. 2. *The discharge activity of two neighboring neurons in the abducens nucleus with spontaneous eye movement.* Shown are the unit discharge and horizontal eye movement. Upward deflection of trace represents eye movement to the right (R). The maintained discharge for unit W-6-3 is not initiated until the eye is deflected almost 20° to the right. By contrast, unit W-6-4 maintained firing is initiated already at a leftward deviation of 20°

To obtain a quantitative measure of (1) initiation of firing relative to eye position and (2) rate at which firing increases, frequency distributions were plotted for each of these two functions. This analysis had to be restricted to units for which the calibration of eye position and the duration of recordings were adequate.

Figure 4 shows the distribution of units in terms of the degree of eye deviation at which they began to fire in a sustained fashion. This measure was obtained by first plotting the discharge frequency of each units as shown in Fig. 3. The point

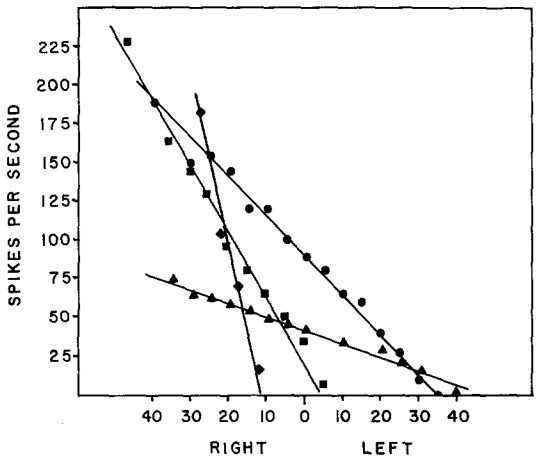

Fig. 3. *Discharge frequency as a function of eye position in orbit for four units in the abducens nucleus*

at which the straight line intersects the zero firing rate was taken as the "cut-in" point. All units (up, down, left, and right) in the oculomotor and abducens nuclei were combined for this purpose. Thus "ON" and "OFF" designate the direction of increasing and decreasing firing rates; firing decreases as the eye moves toward the OFF direction and vice versa. Nine of the units in this sample did not have a "cut-in" point; they maintained their firing rate over the entire eye movement

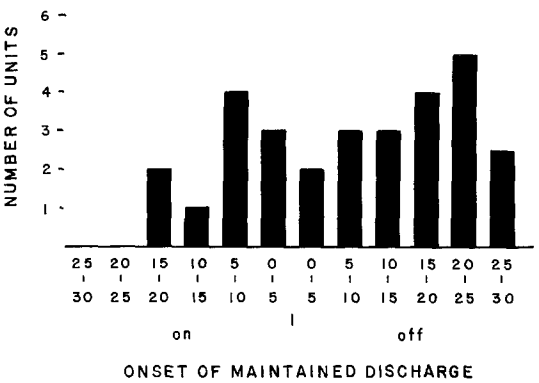

Fig. 4. *Histogram plot of unit discharge initiation for different degrees of eye position in orbit in the oculomotor and abducens nuclei.* The numbers represent groupings in degrees of eye deviation. Firing increase is in the direction denoted as ON

range. The remaining 30 units analyzed in this fashion yielded the distribution shown in Fig. 4. As can be seen, units in our sample seem to be fairly evenly distributed with respect to the onset of firing. However, we have not found units which initiate their discharge at deviations greater than 20°.

The distribution of the rate of firing as a function of eye deviation was obtained in a similar fashion. From this plot we computed, for each unit, the firing

rate increase per degree of eye deviation from frontal gaze. This plot appears in Fig. 5. It shows a somewhat skewed distribution with broad firing rate distribution.

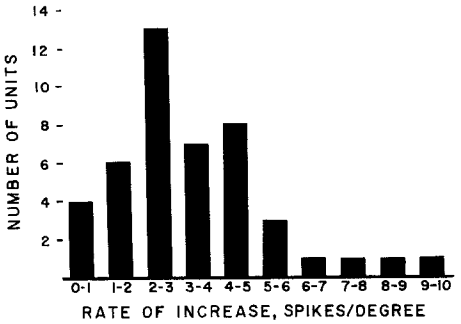

Fig. 5. *Histogram plot of the rate of increase in firing in spikes per degree for units recorded in the oculomotor and abducens nuclei*

b) Quantitative Analysis of Unit Discharge Associated with Saccadic Eye Movement

Next we turn to the discharge activity of these neurons during saccadic eye movement. The inspection of Fig. 1 and 2 reveals that saccadic eye movement is associated with a high frequency burst in unit activity. This burst occurs even when the fixation following the saccade places the eye in a position prior to where the unit would "cut in" for eye position or smooth pursuit. One example of this can be seen in the top right tracings of Fig. 1. In these units, as would be expected, the firing bursts precede the onset of the saccade. It appears that the duration of the saccadic burst is proportional to the size of the saccade.

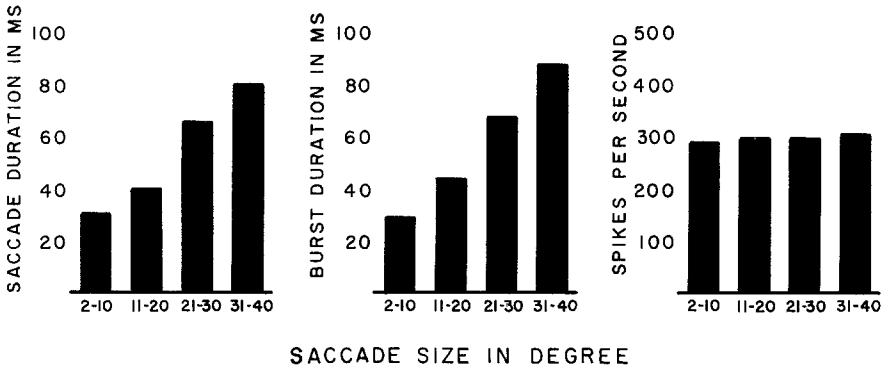

Fig. 6. *Distributions for saccade duration, unit burst duration and unit discharge frequency for saccades of different magnitudes.* Based on one typical unit in the oculomotor nucleus and associated eye movement

In order to clarify the relationship between saccadic eye movement and unit activity, saccade size and duration were compared with unit discharge rate and burst duration. The results of this kind of analysis for one typical unit in the oculomotor nucleus are shown in Fig. 6. The data were obtained by measuring (1) the size

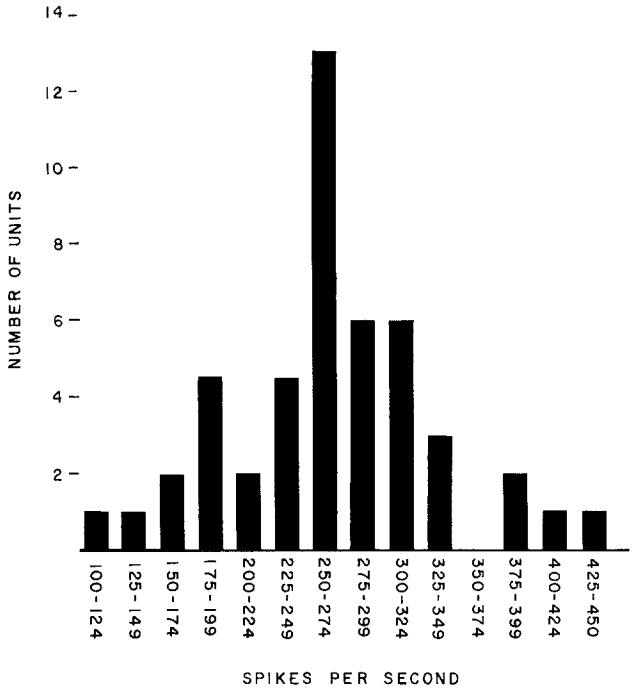

Fig. 7. *Histogram plot of discharge frequency of units during saccadic eye movement*

of each saccade, (2) the duration of the unit burst for each saccade, and (3) the discharge frequency of the unit for each saccade. These data were then pooled for different saccade sizes in 10° steps. Plotting saccade size in degrees against the duration of the saccade (left graph of Fig. 6) shows, as expected, an increasing saccade duration with increasing saccade. The mean duration for saccades corresponds roughly with those found by Fuchs (1967), although the mean rates are slower and the spread is greater. These differences are probably attributable to the fact that the eye movement in our animals was largely spontaneous. The mean rate of the saccades in this sample was 2.68 msec per degree, with a standard deviation of 1.22.

The middle graph in Fig. 6 shows a plotting of the unit burst duration and saccade size. This function is similar to that of the first graph. The correlation between saccade duration and unit burst duration in this sample was +.79 which is significant at the .001 level. The last graph shows the frequency of firing during the saccadic burst as a function of saccade size. The correlation between these two variables was only +.06. These results show that frequency is not associated with saccade size. These findings suggest then that the prime determinant of saccade size is burst duration.

Because we observed that the speed of saccades varies over a small range, it is reasonable to assume that the speed of the saccade may be determined either by firing frequency or by the number of units discharging at a given time. To assess the former, frequency of unit discharge during the saccade was correlated with the average speed of the saccade. This correlation was .38 which was signi-

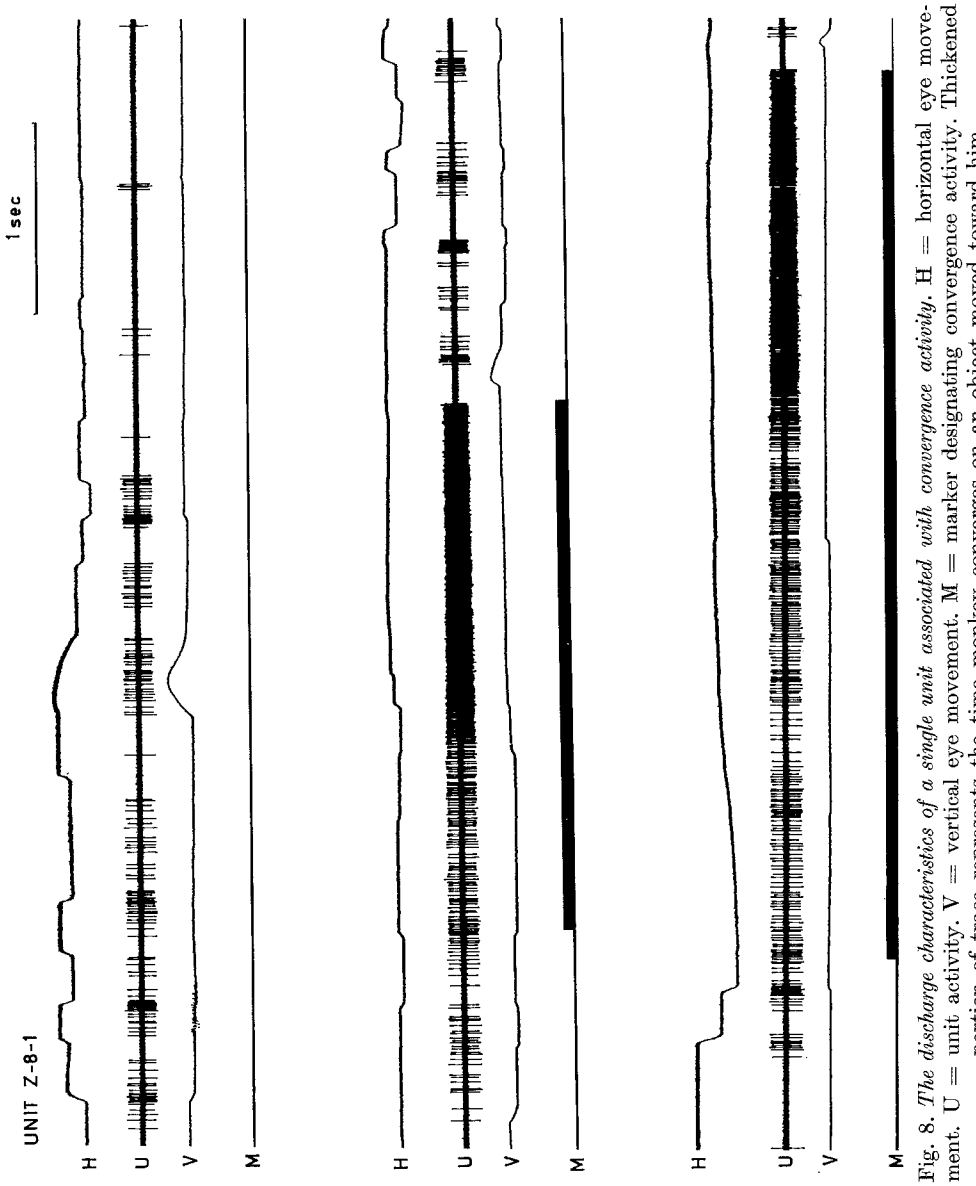

Fig. 8. *The discharge characteristics of a single unit associated with convergence activity.* H = horizontal eye movement. U = unit activity. V = vertical eye movement. M = marker designating convergence activity. Thickened portion of trace represents the time monkey converges on an object moved toward him

ficant at the .005 level. While conclusions from this analysis are tentative, it is likely that the speed of the saccade is determined only in part by discharge rate, and thus may also be regulated by the number of units discharging in synchrony.

In addition to these findings it was also observed that the burst rate associated with saccades varies considerably from unit to unit. Figure 7 shows that the firing rates for the 48 units analyzed exhibit a relatively normal distribution.

We were interested in determining whether or not there is a relationship between saccadic and positional firing rate. To assess this the following analysis was performed: the mean saccadic firing rate of each unit was correlated with

the mean frequency increase per degree of that unit. The 41 units submitted to this analysis showed a correlation of +.48, which was statistically significant at the .005 level.

2. Units Related to Convergence

We have found 7 units which appeared to be related to convergence. Figure 8 showed the response characteristics of one such unit. Both horizontal (H) and vertical (V) eye movement are shown along with the unit (U) in addition to the bottom trace (M) which represents the observed convergence activity of the monkey based on the recorded voice and marker channels. The duration of the signal, as shown by the thickened portion of the line, represents the period of time during which the monkey observed an object such as a piece of food being moved toward him from a distance of about 4 feet to 6—8 inches. The activity of this and other such units failed to show a consistent relationship with respect to direction of eye movement. Convergence on the other hand produces a vigorous response of this sort shown regardless of the angle of approach. When convergence is artificially produced by placing prisms in front of the eye, such units exhibit vigorous discharge for as long as prismatic adjustment is maintained.

Histological examination showed that these units were located in the caudal part of the oculomotor nucleus in the dorsolateral region. We have not observed such units in midline structures. These findings would seem to lend indirect support to Warwick's (1964) contention that the central nuclei are not, as previously asserted (Knies, 1891; Brouwer, 1918), involved in the control of convergence.

3. Other Relationships

In addition to the units so far reported, we have found 14 with characteristics not fitting into any of the above categories. Two of these were clearly related to eye-lid activity. When the lid was closed, these units stopped firing. With the lid open, firing was sustained at a high rate. The discharge characteristics were not affected by light and darkness. These cells probably belong to the nucleus innervating the levator palpebrae.

Ten units had complex characteristics. They responded to both horizontal and vertical eye movement, but not in a one-to-one fashion. It is likely that these units comprise part of the nucleus innervating the inferior rectus which not only rotates the eye but contributes to movement in the horizontal and vertical plane as well (Adler, 1965). Lacking a measure of eye torsion, we were unable to determine the exact characteristics of these units.

Two units could only be described as being inhibited in their sustained firing rate during saccades. These units fired at relatively high rates which were not dependent on eye position. Any saccade was accompanied by a brief inhibition of the discharge activity in these neurons.

Finally, in the region of the abducens nucleus we have recorded units related to vertical eye movement, both up and down. Since the abducens innervated the lateral recti giving rise to horizontal eye movement, these units probably belonged to fiber tracks of passage. In terms of the criteria described on page 9, these units indeed appeared to be fibers. Histology of this area revealed that we were recording from the medial longitudinal fasciculus. The response characteristics of these fibers were in general indistinguishable from those of units in the oculomotor

nucleus. These may be neurons sending their axons to the vestibular nuclei. The alternative possibility that these fibers originate rather than terminate in the vestibular complex raises the intriguing possibility, already suggested by other investigators (Brodal, 1962) that both voluntary and involuntary eye movement may involve the vestibular nuclei.

Discussion

Behavioral investigations have demonstrated that there are two distinct ways in which conjugate eye movement occurs (Rashbass and Westheimer, 1961). The first of these is the saccadic movement which is assumed to serve the function of orienting the fovea to a target in the visual field, and hence may be said to constitute a response to position. The second kind of conjugate eye movement is smooth pursuit which has the function of maintaining a moving target on the fovea and can thus be said to be a response to velocity.

The proposal that different neural mechanisms are involved in the control of these two systems is supported by a number of studies (Dodge, Travis and Fox, 1930; Rashbass and Westheimer, 1961; Young and Stark, 1963; Robinson and Fuchs, 1969). It has been shown that in pathology, damage to certain brain structures can selectively affect one of these systems. Huntington's chorea, for example, produces a selective loss of saccadic eye movements in some cases (Starr, 1966). A similar neural dissociation is suggested in a current study in the unanesthetized monkey by Robinson and Fuchs (1969) which has shown that stimulation of the frontal eye fields yields exclusively saccadic eye movement, suggesting that this area is part of the saccadic control system. In apparent contradiction to these findings, but still supporting such a two systems view, are the single unit recording studies of Bizzi (1968) and Bizzi and Schiller (1969) which have disclosed two types of neurons in the frontal eye fields, one of which responds selectively to saccades and the other to eye position.

Just how far to the periphery such a dissociation may be extended has been open to debate. Results implicating different modes of action have been reported even for extraocular muscles and nerve fibers and have been reviewed by Robinson (1968b). Several investigators have shown that in the cat there are two distinct classes of extraocular muscle fibers having slow and fast twitch response characteristics (Matyushkin, 1961; Bach-y-Rita and Ito, 1966; Hess and Pilar, 1963). Donaldson (1960), examining motor nerve fibers innervating these muscles, found that they fall into two statistical distributions peaking at 3—7 μ and 11—17 μ in diameter.

The results of our investigation indicate that the response characteristics of single units in the oculomotor complex of the rhesus monkey do not form such bimodal distributions. It appears that the two kinds of conjugate eye movement are accomplished by the same set of neurons. Smooth pursuit movement is associated with relatively slow rates of change in firing rate while saccades are associated with rapid bursts of firing in the ON direction in these same units. These findings are in agreement with those reported by Shakhnovich and Nebieridze (1967) who in studying the activity of ocular muscles during nystagmus have found that the same motor neurons are involved in the control of both tracking and saccadic eye movement.

The results of this study have also shown that for most units the firing rate for smooth pursuit activity and for eye position in the ON direction increases in a linear fashion with increase in the angle of eye deviation from straight ahead gaze. The onset of maintained firing for various populations of neurons occurs at different degrees of eye rotation. These observations suggest that smooth pursuit and maintained eye position are brought about by two modes of action: change in the firing rate of units and change in the number of units discharging. Increase in both of these increases the angular deviation of the eye. This relationship is of course reversed for the OFF direction.

Saccadic eye movement is initiated by a rapid burst of firing of units in the ON direction or a corresponding inhibition in the OFF direction. The size of the saccade is determined by the duration of the burst. Discharge frequency, on the other hand, appears to affect the speed of the saccade, which in terms of degrees per millisecond, varies over a relatively small range. Because of the somewhat low, although significant correlation that was found between unit discharge frequency and the speed of the saccade (see page 356), it is likely that the number of neurons discharging in synchrony is also an important determinant of the rapidity with which a saccade is accomplished. Firing rate during the saccadic burst is quite rapid, attaining in some units better than 400 spikes per second. Such high rates of discharge are not uncommon in the mammalian oculomotor complex (Sasaki, 1963; Schaeffer, 1965; Yamanaka and Bach-y-Rita, 1968).

It is interesting to note that a saccade appears to be terminated simply by the cessation of the saccadic burst (accompanied by a cessation of inhibition in nerves supplying the antagonist muscle). We have found no evidence of any "braking action," which if it occurred, should appear as a burst of discharges in the OFF direction after saccadic inhibition. The function of such activity would be to produce a rapid angular deceleration bringing the eye to a sudden stop. Such control is apparently not necessary because of the highly damped nature of the system (Robinson, 1964). This damping seems to be sufficient to stop the eye in the orbit without counteraction, although with saccades in excess of 25° there is evidence that the eye overshoots the target aimed at (Fuchs, 1967). These findings are in contrast with those of Shakhnovich and Nebieridze (1967) who reported that in the rabbit there is an increase in the activity of the antagonist muscle at the end of the saccade which appears to represent the braking action necessary to bring the eye to a sudden stop. This difference may reflect two modes of action in these two species although the possibility of selective sampling in our study cannot be ruled out entirely.

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Prof. Dr. Peter H. Schiller
Dept. of Psychology
Massachusetts Institute of Technology
Cambridge, Mass. (USA)